Mathematical models of ecology and evolution

Analysis of size-structured populations and communities in aquatic ecosystems

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Publication date:
2012

Document Version
Publisher's PDF, also known as Version of record

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– analysis of size-structured populations and communities in aquatic ecosystems

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Academic thesis for the Degree of Doctor of Philosophy at the Technical University of Denmark.
Defense date is February 9, 2012.

Doctoral Thesis
Department of Mathematics
National Institute of Aquatic Resources
Technical University of Denmark, Lyngby, November 2011

First submitted on November 23, 2011
Resubmitted on April 13, 2012

Title of thesis:

Mathematical Models of Ecology and Evolution
– analysis of size-structured populations and communities in aquatic ecosystems

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Preface

The thesis is submitted in partial fulfillment of the requirement for obtaining the degree of PhD at the Technical University of Denmark (DTU). The PhD project was founded partially by the Department of Mathematics (DTU-MAT) and partially by the National Institute of Aquatic Resources (DTU-AQUA) and finally by Globalization funds. The project was carried out as a collaboration between DTU-MAT and DTU-AQUA in the period from September 1st 2008 − November 23rd 2011 under the supervision of Kim Knudsen (DTU-MAT), Ken Haste Andersen (DTU-AQUA) and Uffe Høgsbro Thygesen (DTU-AQUA).

I would like to thank all my supervisors for their guidance and help throughout the duration of study. I really enjoy working with them and greatly appreciate their patience and encouragement whenever I was confronted with trouble and frustration. Particular thanks go to Ken Haste Andersen who has spent huge amount of time on guiding my research.

I wish to thank Ulf Dieckmann and Åke Brännström for giving me a precious opportunity to study at the International Institute for Applied System Analysis (IIASA) in Vienna, where I learned adaptive dynamics which makes an important contribution to this thesis. Also, I want to give my great thanks to Michael Pedersen and Zhigui Lin who provided me with the opportunity to study as a PhD student at DTU, a key turning point in my life.

I want to thank all my colleagues at DTU-MAT and DTU-AQUA, especially Martin Hartvig for helpful discussions about fish ecology, valuable suggestions on writing biological papers and great help in writing this thesis, Victor Manuel Rodriguez Zermeno for all kinds of discussions. Michael, Frank, Morten, Peter, Manh, Mohamed and Valerie are also thanked for your hospitality and for including me as one of your own. Those days spent at these two departments are never to be forgotten. I also want to thank my Chinese friends, Ling, Tian and Tang for additional cooperation and support. My final thanks go to my family, especially my wife, for their continuous support right from the start of my study.

Lai Zhang

November 2011
Lyngby, Denmark

List of papers

The thesis is based on the following four papers, referred throughout the text by their roman numerals:

I Lai Zhang, Zhi Gui Lin, Michael Pedersen (2012). Effects of growth curve plasticity on size-structured population dynamics. *Bulletin of Mathematical Biology* 74, 327-345.

II Lai Zhang, Martin Hartvig, Kim Knudsen, Ken Haste Andersen (2011). Relationship between food-web and size-spectrum representations of communities (manuscript).

III Lai Zhang, Uffe Høgsbro Thygesen, Kim Knudsen, Ken Haste Andersen (2012). Trait diversity promotes stability of community dynamics. *Theoretical Ecology*, doi:10.1007/s12080-012-0160-6.

IV Lai Zhang, Ken Haste Andersen, Ulf Dieckmann, Åke Brännström (2011). Four types of interference competition and their impacts on the ecology and evolution of size-structured populations and food webs (manuscript).

Other papers written during the 3-year PhD study:

1. Zhi Gui Lin, Michael Pedersen, Lai Zhang (2010). A predator-prey system with stage-structure for predator and nonlocal delay. *Nonlinear Analysis: Real World Application* 72, 2019-2030.
2. Can Rong Tian, Lai Zhang, Zhi Gui Lin (2011). Pattern formation for a model of plankton allelopathy with cross-diffusion. *Journal of the Franklin Institute* (in press) doi: 10.1016/j.jfranklin.2011.05.013.
3. Jia Liu, Hua Zhou, Lai Zhang (2011). Cross-diffusion induced Turing patterns in a sex-structured predator-prey model. *International Journal of Biomathematics* doi: 10.1142/S179352451100157X.
4. Qin Lin Tang, Lai Zhang, Zhi Gui Lin (2011). Asymptotic profile of species migrating on a growing habitat. *Acta Applicandae Matematicae* (in press) doi: 10.1007/s10440-011-9639-1.

Resumé

Forståelsen af dynamik og strukturer i arts-populationer og -samfund hører til blandt de vigtigste udfordringer i den økologiske teori. Denne afhandling undersøger hvordan disse højniveau-processer er influeret og styret af økologiske og evolutionære processer påindividuelt (lavt) niveau. Disse individuelle processer er parameteriseret med individuel kropsstørrelse. Kropsstørrelse er en af de vigtigste karakteristikker ved et individ, da den bestemmer kvalitative og kvantitative forhold mellem individer, samt de hastigheder hvorved de fleste livs-historie processer finder sted. Ved at karakterisere arter og deres livshistorie med traits undersøges forholdet mellem individuelle processer og egenskaber påartssamfundsniveau.

Artikel I undersøger hvordan to forskellige individuelle energifordelingsmekanismer, net-optagelse ($\kappa-$reglen) og størrelsesafhængig net-reproduktion, påvirker dynamikken mellem en størrelses-struktureret consumer, Daphnia, og en ikke-struktureret alge-ressource. Det konkluderes at i forhold til den første mekanisme forårsager den anden mere ustabil populationsdynamik mod at den til gengæld øger sandsynligheden for artseksistens ved at forkorte den juvenile tid mellem fødsel og reproduktionsmodning. Artikel II sammenligner størrelses-spektrum og fødenetværks repræsentationer af økologiske artssamfund via en trait-baseret (kropsstørrelse og habitat lokation) ikke-struktureret Lotka-Volterra model, og viser at de to modeltyper resulterer i artssamfund med meget ens karakteristika. Artikel III undersøger hvordan vækstforskelle mellem arter (styret af et trait: asymptotisk kropsstørrelse) påvirker dynamikken af marine økosystemers størrelsesspektrum. Det påvises at den trait-inducerede vækstvariabilitet udvider det parameterområde hvori ligevægtspunktet er stabilt, samt at den ikke-lineære dynamik udenfor ligevægtsområdet får mindre, mere regulære og langsomme oscillationer. Artikel IV introducerer fire typer tæthedsafhængig interferens-konkurrence der finder sted påindivid-niveau (styret af et trait: reproduktiv modningsstørrelse) og påvirker individuel foragering, stofskifte, overlevelse, eller rekruttering. Det undersøges hvordan de forskellige interferens-typer påvirker økologien og evolutionen af størrelses-strukturerede populationer. Økologisk set påvirker interferens demografiske egenskaber positivt eller negativt afhængigt af balancen mellem interferensinduceret energioptag og de energetiske omkostninger. Evolutionært set kan reproduktiv modningsstørrelse mindskes (foragering- og stofskifteinterferens) eller øges (overlevelse- og rekrutteringsinterferens) i et monomorfisk miljø. Yderligere vises det, at blandt de fire interferenstyper resulterer overlevelsesinterferens oftest i store komplekse fødenetværk gennem gradvis evolution og artsdannelse.

Abstract

Understanding the dynamics and structure of populations and communities is one of the most important challenges in ecological theory. The thesis consists of theoretical investigations of how these phenomena at high level are influenced by the ecological and evolutionary processes occurring at low level (i.e. individual level). Individual-level processes are all parameterized with body size. Being one of the important characteristics of individual organisms, body size determines the qualitative and quantitative relationships among individuals, and influences most, if not all, key life-history processes. By characterizing species and life history with traits, the interrelationship between community-level properties of ecological interest and individual-level performance is explored.

Paper I examines the influences of two different mechanisms of energy partitioning among individual life-history processes: net-assimilation mechanism of $\kappa-$rule and net-reproduction mechanism of size dependence using a simple model comprising a size-structured consumer *Daphina* and an unstructured resource *alge*. It is found that in contrast to the former mechanism, the latter tends to destabilize population dynamics but as a trade-off promotes species survival by shortening juvenile delay between birth and the onset of reproduction. Paper II compares the size-spectrum and food-web representations of communities using two traits (body size and habitat location) based unstructured population model of Lotka-Volterra type and shows a robust reconciliation between the two representations. Paper III investigates the effects of growth variability induced by the trait (maximum body size) on the dynamics of marine size spectrum. It shows that the introduction of trait expands the set of parameters for which the equilibrium is stable, and if the community is unstable, the non-linear non-equilibrium dynamics has much smaller, slower, and more regular oscillations than if trait is excluded. Paper IV develops four types of density-dependent interference competition at the individual level in a trait (size at maturation) based size-structured population model, that is, interference in foraging, maintenance, survival, and recruitment. Their impacts on the ecology and evolution of size-structured populations and communities are explored. Ecologically, interference affects population demographic properties either negatively or positively, depending on the balance between interference induced gain and cost. Evolutionarily, the maturation size is either depressed (interference in foraging and maintenance) or elevated (interference in survival and recruitment) in a monomorphic population environment. Moreover, among the four interference mechanisms, survival interference is more likely to produce large communities with complex trophic patterns through gradual evolution and successive speciation.

Contents

Mathematical Models of Ecology and Evolution

– analysis of size-structured populations and communities in aquatic ecosystems

Community ecology is often perceived as a "mess", given the seemingly vast number of process that can underlie the many patterns of interest, and the apparent uniqueness of each study system. However, at the most general level, patterns in the composition and diversity of species – the subject matter of community ecology – are influenced by only four classes of process: selection, drift, speciation, and dispersal.

Vellend (2010)

1 General introduction

Ecology describes the relationships among organisms, and between them and the environment, thus determining aspects such as species abundance, compositions of a biological community that represents a group of organisms living in a specified place and time. Evolution describes the processes governing the gene pool of a population from generation to generation through processes such as mutation, natural selection, and genetic drift, thus controlling the patterns like trait and genetic compositions. Ecology and evolution jointly govern the dynamics of ecosystems, create the biological diversity in both time and space. In this thesis, I consider the dynamics and structure of populations and communities from both ecological and evolutionary perspectives, using mathematical models as conceptual frameworks.

The mathematical models employed in this thesis are all developed at the individual level due to the fact that it is individuals rather than species that interact directly (Hartvig, 2011) in the forms such as predation and competition. Community-level properties are envisaged as emergent results of the individual-level processes (Polis and Strong, 1996) and obtained through bookkeeping individual-level events. Such

an approach has advantages. One is that more mechanistic details of individual physiology can in principle be incorporated into models (Diekmann and Metz, 2010), making it possible to capture the complexity of nature in a more coherent manner. While maintaining a consistent and complete deterministic bookkeeping scheme for sufficiently large populations (Metz and Diekmann, 1986), models encapsulate a relatively high biological realism.

Another advantage is that individual-based models allow for intra-species variation when individual taxonomic identity is taken into account. Within the same species individuals might differ in many aspects such as structure, physiology and mortality. As an example, consider the Atlantic cod, which is around one milligram at birth but could grow up to kilogram at maturation, spanning more than 5 orders of magnitude in size (Andersen et al., 2008). Over this course, cod individuals will experience several trophic levels, thus facing a tremendous risk of being eaten before maturation when they conversely consume the species that previously prey on larvae cods like herring, leading to ontogenetic trophic niche shift (Werner and Gilliam, 1984). Since intra-species variation has significant effects on population dynamics (Neill, 1988; Persson, 1988; Werner, 1988; de Roos et al., 1990; Orr et al., 1990; Perrson et al., 1998; Claessen et al., 2000; de Roos et al., 2003; Claessen and de Roos, 2003), structured population models have been developed to disaggregate individuals within species including stage-, age- and physiological-structured models (Gurney et al., 1983; Nisbet and Gurney, 1983; Metz and Diekmann, 1986; de Roos et al., 1992, 1997; Cushing, 1994, 1998; de Roos and Persson, 2001; Hartvig et al., 2011). In this thesis, I mainly adopt the physiological-structured population models and apply them to aquatic ecosystems.

Among individual physiological characters, body size (i.e. body mass) plays a key role across multiple scales of biological organizations from the individual to ecosystem. At the individual level, body size is a major factor of constraining the structure and functioning of organisms, in particular the bioenergetic requirements (Brown et al., 2004), and influences many life processes like movement and food consumption (Ware, 1978), growth (Gillooly et al., 2002), fertility (Wootton, 1977; Andersen et al., 2008), and dispersal ability (Eklöf, 2009), and further determines population abundance (Nee et al., 1991; Cohen et al., 2003), home range (Kramer and Chapman, 1999; Haskell et al., 2002; Jetz et al., 2004), trophic position (Jennings et al., 2001), and relationship with other members of ecological community (Jennings et al., 2002; Barnes et al., 2010). At the ecosystem level, body size has profound effects on the patterns and dynamics of food webs as well as other ecological networks (Woodward et al., 2005). In aquatic ecosystems, body size is negatively correlated with individual abundance with a power-law relationship (Boudreau and Dickkie, 1992; Cohen et al., 2003). Inspired by the size-based approach, all physiological rates of individuals in my models are scaled with body size using the allometric scaling relationship (Peters, 1983), specifying the physiological-structured population models to the size-structured population models (e.g. de Roos and Persson, 2002; Claessen and de Roos, 2003; Hartvig et al., 2011).

Mathematically, size-structured population models are formulated as partial dif-

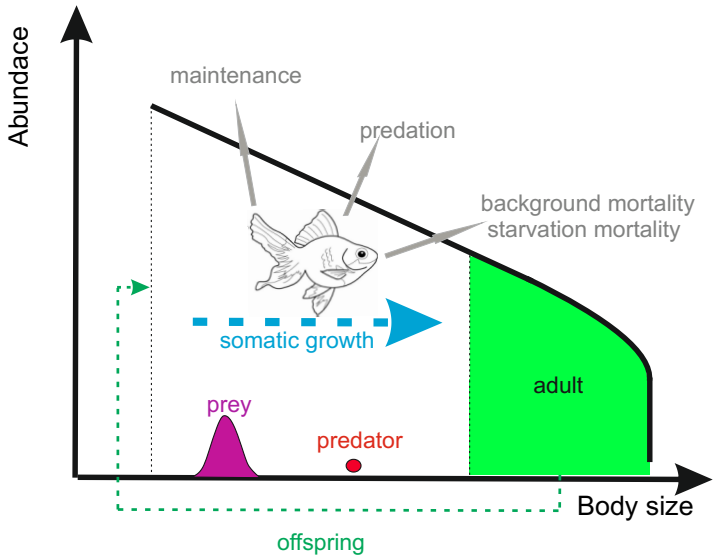

Fig. 1: Graphical interpretation of the size-structured population model (Hartvig et al., 2011) (only one species is explicitly presented). The model describes the distribution of individual abundance as a function of body size (bold curve). Individual changes body size through somatic growth and experiences maintenance and mortality (predation, background and starvation). Reproduction from all mature individuals (green area) enters through the boundary conditions as a flux of offspring (green lines). Most importantly, predation is entirely size-based and a consumer individual (red cycle) preys upon small individuals of size with a limited range in relation to its body size (purple area, the feeding kernel). Mathematical formulations of the population dynamics and offspring recruitment, of the predator-prey interaction, and of the life-history processes such as maintenance, growth and mortality refer to Box 1, 2 and 3, respectively.

ferential equations known as the McKendrick-von Foerster equations (McKendrick, 1926; von Foerster, 1959). The formulation could take place at two levels. In the first, it describes the population dynamics with species identity being taken into account. By resolving individual life history, the formulation yields a density distribution against individual body size within a species, generally referred to as species size spectrum (de Roos et al., 1990; Claessen and de Roos, 2003; Andersen and Beyer, 2006; Hartvig et al., 2011; Hartvig, 2011; Hartvig and Andersen, 2011). In the second, it demonstrates the community dynamics directly and yields the relationship between individual abundance versus body size irrespective of species taxonomic identity, generally referred to as community size spectrum (Sheldon and Parsons, 1967; Sheldon et al., 1972; Silvert and Platt, 1980; Benoît and Rochet, 2004). However, in the former case, the community size spectrum can be obtained indirectly by summing all the size spectra of species that coexist in the communities (Andersen and Beyer, 2006; Hartvig et al., 2011).

The individual-based size-structured population models have recently been a subject of intensive research. They have been used to explore the impacts of fishing

on marine communities (Benoît and Rochet, 2004; Andersen and Pedersen, 2010; Rochet and Benoît, 2011), the role of cannibalism on population stability (Claessen and de Roos, 2003), intraguild predation (Hartvig and Andersen, 2011), demographic properties and stability of marine size spectrum (Andersen and Beyer, 2006; Law et al., 2009; Datta et al., 2010, 2011; Plank and Law, 2011; Arino et al., 2004; Capitán and Delius, 2010; Blanchard et al., 2009). In this thesis, the size-structured population models are the foci, and I employ them to investigate the influences of ecological performance at the level of individuals on the patterns at the level of populations and communities. A conceptual figure (Fig. 1) is presented for the intuition on the size-structured population model.

1.1 Ecological objectives

The essential task of the thesis is to understand community-level phenomena from the ecological performance of individuals. As there are numerous high-level patterns as well as low-level processes, in this thesis the low-level ecological performance pertains to the size-based interactions (i.e. predation and competition) and life-history processes (i.e. feeding, growth, maintenance, reproduction) and the community-level properties merely involve several aspects of size spectra and food webs. Specifically, the following questions are addressed in four papers:

Q1: What are the impacts of different mechanisms of energy partitioning among individual life-history processes on size-structured population dynamics (Paper I)?

Q2: To which degree can the size-spectrum community representations be reconciled with the food-web community representations (Paper II)?

Q3: How does the trait-induced growth variability among individual life history affect the stability and dynamics of marine size spectrum (Paper III)?

Q4: How to develop individual-based interference competition as opposed to species-based interference in size-structured population models (Paper IV)?

Q5: What are the evolutionary responses of individual maturation size to population feedback (Paper IV)?

Q6: How do complex food-web communities emerge evolutionarily from low-level processes such as predation and competition (Paper IV)?

More precisely, Paper I focuses on the the strategy of energy distribution among size-dependent life-history traits and its influence on the stability of equilibrium solutions in a simple community comprising a size-structured consumer and an unstructured resource. Two strategies of net assimilation and net reproduction are compared (Lika and Nisbet, 2000). The discrepancy between two strategies lies in the assumption concerning the way in which absorbed energy is channelled to

reproduction: absorbed energy minus reproduction in the former strategy while absorbed energy minus maintenance in the latter. Paper II considers the relationship between the two community representations, i.e. size-spectrum and food-web representations, which have been studied heavily but historically separately. However, as different representations of the same underlying community, results should be compatible. Paper III examines the influence of growth variability among individuals of the same body size but belonging to different species on the dynamics of marine size spectrum. It is motivated by the recent finding that growth variation has a stabilizing effect on equilibrium size spectrum in the deterministic jump-growth models (Datta et al., 2010; Plank and Law, 2011). The mechanism accounting for the growth variability in their models is a consequence of stochastic feeding event, and differs radically from the mechanism here, which is a deterministic result from the inclusion of species identity. The last paper develops four types of density-dependent interference competition at the individual level in a trait-based size-structured population model, and explores their impacts on the ecology and evolution of populations and food webs. Particularly, the emergence of food webs through evolution and speciation has been considered with unstructured population models (e.g. Loeuille and Loreau, 2005; Brännström et al., 2010), but not touched to date with structured populations.

1.2 Mathematical modelling

To address above questions, four mathematical models are developed: an unstructured population model (Paper II), a continuously size-structured population model for single species (Paper I), a trait-based marine size-spectrum model (Paper III), and a trait-based food-web model with size-structured populations (Paper IV). Basically, these models can be classified into two categories: unstructured population models and size-structured population models. Mathematically, the dynamics of unstructured populations are described by a set of ordinary differential equations (ODEs) of Lotka-Volterra type while the dynamics of structured populations are governed by a set of partial differential equations (PDEs) which are known as the McKendrick-von Foerster equations (Box 1).

The unstructured population model is built on the consumer-resource model in Yodzis and Innes (1992), which was developed using bioenergetic approaches. The advantage of this model is its generality as most parameters are not species-based but scaled allometrically with the body size of individual organisms. Although it is not a food-web model, its generality of parameterization makes it possible to be extended to a food-web framework. Paper I follows this direction and characterizes individuals with two traits: body size and habitat location. Habitat trait represents a spatial distribution of individuals and determines the coefficients of interaction among individuals in conjunction with body size (i.e. r_i and α_{ij} in equation (1) in Box 1).

The three size-structured population models are essentially derived from the trait-based size-spectrum model in Andersen and Beyer (2006). The model was

Box 1: Population dynamics

Unstructured population models (Lotka, 1925; Volterra, 1926)
Population dynamics are described by a set of ordinary differential equations:

$$\frac{dN_i}{dt} = N_i \left(r_i + \sum_j \alpha_{ij} N_j \right), \tag{1}$$

where N_i represents the density of unstructured population i; r_i is the intrinsic per capita growth rate and generally positive for resource species; α_{ij} is the interaction coefficient, reflecting the per capita effect of species j on the per capita growth rate of species i, exerted by, for instance, predation or interspecific competition. An important extension of this model is the consumer-resource model in Yodzis and Innes (1992) who scaled the coefficients with body size based on the bioenergetic approaches. Paper I is built on this model, but those interaction coefficients are jointly determined by body size and habitat location (see Box 2 in the section of *Individual-level interactions*).

Remarks: The fundamental assumption is instantaneous reproduction of offspring and mortality as a result of predation and/or competition.

Size-structured population models (Andersen and Beyer, 2006)
Population dynamics are governed by a set of partial differential equations:

$$\frac{\partial}{\partial t} N(w, M, t) = -\frac{\partial}{\partial w}(g(w, M, N_c) N(w, M, t)) - \mu(w, N_c) N(w, M, t) \tag{2}$$

with a boundary condition representing the flux of w_0-sized offspring (Hartvig et al., 2011) (the flux of offspring in Fig. 1):

$$N(w_0, M, t) = \int b(w, M, N_c) N(w, M, t) dw, \tag{3}$$

where $N(w, M, t)$ is the density distribution of w-sized individuals at time t for the species of trait M, i.e. maximum body size; $g(w, M, N_c)$, $\mu(w, N_c)$ and $b(w, M, N_c)$ are three life-history processes: somatic growth, mortality and fertility, which are density-dependent. $N_c(m) = \int N(w, M, t) dM$ (Andersen and Beyer, 2006) or $N_c(m) = \sum_M N(w, M, t)$ (Hartvig et al., 2011) is the community size spectrum obtained by summing all size spectra of species existing in the community.

Remarks: In the models, predation causes instantaneous somatic growth and mortality. Population is recruited by the reproduction of adults with size beyond a prescribed value. Equation (2) is known as the McKendrick-von Foerster equation (McKendrick, 1926; von Foerster, 1959). Such type of model is used in Paper I, III and IV. The three life-history rates are specified in Box 3 in the section of *Life history*.

designed for marine ecosystems and used a trait (i.e. maximum body size) as representation of species (Norberg et al., 2001; Bruggeman et al., 2007; Merico et al., 2009). The maximum body size indicates the maximally attainable individual body size. Population dynamics is described through the McKendrick-von Foerster equation (equation (2) in Box 1). Moreover, the boundary condition representing the recruitment of offspring is not modeled due to the assumption of the continuum of trait which varies from zero to infinity. Paper III restricts the trait to a finite range that spans around 10 orders of magnitude (Cohen et al., 2003) and prescribes a size for offspring, that is, $w_0 \sim 1$ milligram (Andersen et al., 2008) (Box 1). The offspring size is assumed to be the same for all species. However, the boundary condition of offspring recruitment is assumed to be constant over time.

The dynamics of offspring recruitment (equation (3) in Box 1) is explicitly modeled by Hartvig et al. (2011) who extended the trait-based size-spectrum model (Andersen and Beyer, 2006) to a food-web model. In addition to the difference regarding the boundary condition, the two models differ also in the number of interacting species. In the former model, species is continuous in trait (i.e. infinite number of species), but in natural communities, species are more likely to be discrete in the trait space (i.e. finite number of species). Thus, the trait-based food-web model is more relevant. Paper IV employs the food-web model but refines it by incorporating interference competition which is developed for the first time in a size-structured population model at the individual level. Paper I also uses the trait-based food-web model, whereas there is only one structured species.

To summarize, although the four models differ in several aspects, they preserve three common features: (i) all models are parameterized at the individual level as opposed to the species level and designed for aquatic ecosystems; (ii) body size governs individual ecological performance and is used for allometric scaling of individual physiological rates; (iii) predation is the direct force driving population dynamics.

1.3 Mathematical tools

As either there are many interacting species (Paper II, III and IV) or species are continuously size-structured (Paper I, III and IV), analyzing above models is mathematical challenging. Nevertheless, there are mainly four mathematical approaches: parameter continuation (Paper I, III), ecological community assembly (Paper II), automatic differentiation (Paper III), and evolutionary community assembly (Paper IV). These methods are in principle based on numerical calculation.

Paper I considers an size-structured consumer species competing for an unstructured resource. Mathematically, the model consists of a PDE describing the dynamics of consumer species and an ODE describing the dynamics of resource. The two equations can be reduced to a system of two delay equations (a renewal equation for the birth rate of consumer population coupled to a delay differential equation for the resource species) (Diekmann and Metz, 2010). From the delayed-differential equations, equilibrium solutions can be expressed implicitly and the characteristic equation, determining the stability of equilibrium solutions, can be derived analyti-

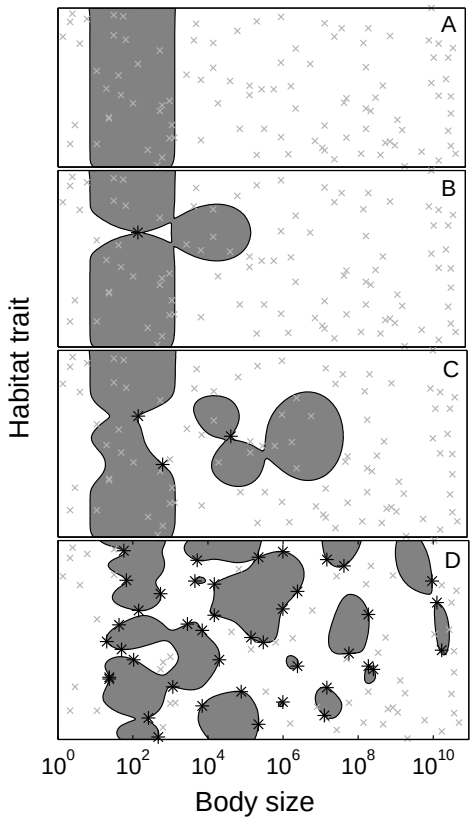

Fig. 2: Assembly of a model community from a finite pool of 100 species (light grey crosses). (A) Fitness landscapes of the pristine environment showing areas where the invasion fitness is positive (grey), (B) after the first successful invasion, (C) after the third successful invasion, and (D) in the final un-invadable end-state (as no species in the species pool have trait values in the grey areas). Positive invasion fitness are indicated by the grey areas outside which invasion fitness is negative. Successful invaders (stars) sit on the boundaries of the grey islands where fitness is zero. In the final assembled community 42 species coexist. Details of this figure refers to Paper II.

cally (Diekmann et al., 2007). However, it is not trivial at all to solve the equilibria and determine their stability as ingredients, involved in the equilibrium solutions and the characteristic equations, are presented in the form of integral. Defined as solutions of ODEs, these integrals are able to be evaluated. Hence, equilibrium solutions can be computed and their stability can be determined. With two selected free parameters, the boundaries of coexistence (i.e. consumer coexists with resource) and stability (i.e. different regions with stable and unstable equilibrium solutions) in the two-dimensional parameter space can be traced using the technique of parameter continuation (Kuznetsov, 1994; de Roos et al., 2010).

Paper II obtains communities using ecological community assembly (Law and Morton, 1996; Law, 1999; Virgo et al., 2006). The method is graphed in Fig. 2 and the detailed algorithm of assembly is included as an appendix in this paper.

The idea of this approach is as follows. Ecological communities, comprising a set of species, not arise in a single step but rather emerge through the invasion of species that migrate sequentially from a predetermined species pool (light crosses in Fig. 2). The invasion starts with a pristine community in which there is only resource (Fig. 2A). Species is chosen one at a time randomly from the species pool and introduced into the community, forming an augmented community. The next species is introduced only after the augmented community has reached a state when there are no changes in community composition, although population properties are still changing locally (Fig. 2B, C). Over this course, the invader may survive or fail to colonize. Each outcome is likely to be accompanied with extinctions of one or more native species. A community ultimately appears when no species in the species pool are able to invade (Fig. 2D). The emergent communities are then used to analyze community-level patterns such as the size-spectrum exponent, trophic level and invasion stability.

Paper III looks into the linear stability and nonlinear dynamics of marine ecosystems modeled through a trait-based size-spectrum model (Andersen and Beyer, 2006), which is formulated as a set of PDEs. To find equilibrium solutions, individual body size and the trait are divided into discrete individual size groups and trait groups. The PDEs are discretized using the upwind semi-implicit scheme (Hartvig et al., 2011). This discretization transforms the PDEs into a system of ODEs. Equilibrium can be found using Newton's method (Kuznetsov, 1994). The stability of the equilibrium can be determined by the maximum real part of the eignevalues of the Jacobian matrix for the system of obtained ODEs. Varying parameter values, equilibrium can be traced continuously (Kuznetsov, 1994). It is worth pointing out that when computing the Jacobian matrix, the derivatives of the matrix entries with respect to variable (i.e. size group) can be derived manually and evaluated by inserting the equilibrium solution into the derived form straightforwardly, an approach we call automatic differentiation. The details of this approach is given as an appendix of Paper III.

Paper IV explores, from the evolutionary point of view, the emergence of communities with size-structured populations. Dynamics of populations are described through a set of PDEs. Communities are obtained via evolutionary community assembly (Brännström et al., 2010). The fundamental discrepancy between ecological and evolutionary community assembly is that the evolutionary assembly approach does not involve the concept of species pool and new species arise as a consequence of evolution (Dieckmann and Law, 1996) and speciation (Geritz et al., 1998). This method is illustrated graphically in Fig. 3A. Evolution starts from an ancestor, and is driven by ecological interactions such as predation and competition which take place on the ecological time scale. Mathematically, the evolutionary trajectory of each species is described through a canonical equation (Dieckmann and Law, 1996), which governs the evolutionary fitness of each species. Speciation comes about when the fitness of a species is a minimum on the fitness curve (Geritz et al., 1998). An community (Fig. 3B) emerges when there is no possibility for speciation. Importantly, speciation occurs on the evolutionary time scale which is several orders of

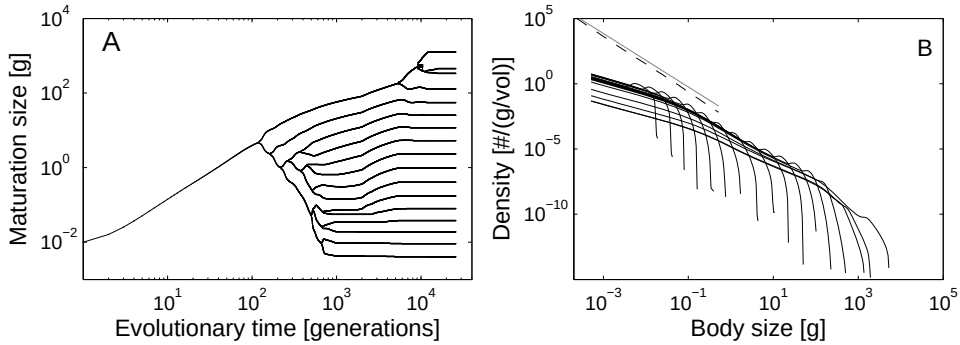

Fig. 3: An example of community assembly in a species-speciation model where species are characterized by a trait, i.e. maturation size. Through gradual evolution and continuous speciation, a community comprising 17 species ultimately appears (A), and their size spectra are illustrated with black curves in panel (B) where grey curves indicate the initial (solid) and final resource spectrum (dashed). In this model, the ecological time scale, which is on the same order of magnitude as population life time, is strictly separated from the evolutionary time scale, which is several orders larger. Details of this figure refer to Paper IV.

magnitude larger than the ecological time scale. Thus, the ecological interactions are assumed to be strictly separated from the evolutionary dynamics (Dieckmann and Law, 1996). Detailed description of this method is appended to this paper.

1.4 Ecological findings

In response to the questions proposed previously, brief answers go as follows:

A1: In contrast to the net-assimilation model, net-production model tends to destabilize population dynamics but promotes species coexistence by avoiding juvenile bottleneck (Paper I).

A2: There is a robust reconciliation between food-web and size-spectrum representations especially in terms of size-spectrum exponent in particular for species-rich communities (Paper II).

A3: Trait-induced growth variability among individuals of the same body mass but with different taxonomic affiliation stabilizes marine size spectrum (Paper III).

A4: Four types of density-dependent interference competition are developed according to their effects on individual ecological performance (interference in foraging, maintenance, and survival) and offspring recruitment (interference in recruitment) (Paper IV).

A5: In a monomorphic population environment, individual maturation size is either depressed (interference in foraging and maintenance) or elevated (interference in survival and recruitment) (Paper IV).

A6: Food-web communities can arise based on simple ecological (predation and competition) and evolutionary (adaptive changes in fitness) rules. Among the four interference mechanisms, survival interference promotes the emergence of species-rich communities with complex trophic patterns (Paper IV).

The thesis is structured as follows. The introductory part of this thesis *Mathematical Models of Ecology and Evolution* first gives an overview in the section of *General introduction* (Section 1). As the essence of this thesis is the interplay between individual performance and community patterns, I describe these two aspects in three sections termed as *Individual-level processes* (Section 2), *Scaling from individuals to the level of population* (Section 3), and *Community-level patterns* (Section 4). The section of *Individual-level processes* describes individual-level interactions including predation and competition (Section 2.1), and life-history processes (Section 2.2). The section of *Community-level patterns* depicts the widely observed community properties including species diversity, stability, trophic level and size distribution. The connection between ecological performance of individuals and community-level patterns are bridged via the scaling from individuals to populations, which is presented in Section 3. Along with the description, relevant representations (e.g. boxes, graphics or tables) are provided to facilitate understanding. The introductory part ends up with a section of *Conclusions* (Section 5) describing the contributions of this thesis to ecological theory (Section 5.1), ecological perspectives (Section 5.2), and mathematical challenges (Section 5.3). A brief overview of each paper is presented in *Summary of papers*. All papers are included in the back of this thesis.

2 Individual-level processes

In this section, I discuss two individual-level interactions (i.e. predation and competition) and individual life history in separate subsections. The first subsection begins with a description of size-dependent feeding interaction, followed by an introduction of competition consisting of exploitative competition and interference competition. A short summary of interference competition in unstructured population models is presented and I further describe two advantages of developing size-based interference competition at the individual level, which is carried out in Paper IV. The second subsection first depicts the background of individual life history as well as its effects on the dynamics and structure of populations and communities, and then gives its understanding in the context of Dynamic Energy Budget theory, and finally shows the motivation of comparing the net-assimilation and net-reproduction energy strategies, which is conducted in Paper I.

2.1 Individual interactions

Predation and competition are two of the most important types of ecological interactions among species and thought to be crucial in determining the structure of natural communities (Diamond and Case, 1986; Kotler and Holt, 1989; Morin, 1999;

Chase et al., 2002; Chesson and Kuang, 2008). While Chase et al. (2002) argued that competition for resource is seen as a primary interaction constraining species diversity and predation just modifies competitive behaviors, Chesson and Kuang (2008) claimed that predation and competition have equal potential to influence diversity maintenance. Despite the fact that the two species-based interactions dominate studies in population and community ecology, it should be clearly recognized that species-based interactions are theoretically abstract and in fact are the resultant of individual-level interactions (Hartvig, 2011). Thus, in light of the growing evidence of size-based processes occurring at the individual level, a shift from species-based interactions to individual-based interactions is being considered.

Predation in this thesis is size-based irrespective of the taxonomic identity of individual organisms, as body size has long been recognized to be one of the most obvious and important features of any animal (Peters, 1983; Cohen et al., 1993). Affecting not only the amount of energy an individual organism demands for metabolism (Brown et al., 2004), the attack rate, and also the probability of avoiding being eaten by other organisms, body size significantly governs the type and strength of predation between differently sized individuals. In natural communities, empirical data discloses a general pattern that individuals are larger than their victims (Warren and Lawton, 1987; Cohen et al., 1993; Brose et al., 2006b; Barnes et al., 2010), or in other words, it can be rephrased as "large individuals eat smaller ones". This simple "big-eat-small" rule can be mathematically formulated by a feeding kernel with two free parameters (equation (4) in Box 2). One parameter decides the geometric mean prey size of a predator, or alternatively the preferred predator-prey mass ratio (PPMR), and the other governs the range of prey size, or alternatively, the width of feeding kernel (Claessen and de Roos, 2003; Benoît and Rochet, 2004; Andersen and Beyer, 2006; Law et al., 2009; Hartvig et al., 2011). Such formulation is additionally supported by stomach analyses (Ursin, 1973, 1974).

Empirical data on size-dependent predation further shows that the preferred PPMR increases with body size and the width of feeding kernel is wider for larger organisms than for smaller ones (Cohen et al., 1993). For a limited size range (i.e. 2-2048 gram), Jennings et al. (2002) found that the preferred PPMR varies slightly with the body size of organisms. Such constant preferred PPMR has been ever assumed in many theoretical studies (e.g. Benoît and Rochet, 2004; Loeuille and Loreau, 2005; Andersen et al., 2008, 2009; Law et al., 2009; Andersen and Pedersen, 2010; Datta et al., 2010; Brännström et al., 2010; Rochet and Benoît, 2011). Nevertheless, Barnes et al. (2010) showed that the preferred PPMR correlates with body size in a power-law relationship by aggregating data across the whole marine size spectrum from a certain amount of locations in the world.

Theoretical studies demonstrated the profound effects of such size-selective predation on the dynamics of both populations and communities. It can drive alternative steady state (Claessen and de Roos, 2003; Hartvig and Andersen, 2011) and initiate catastrophic collapse of top predators (de Roos and Persson, 2002). In marine ecosystems, the whole size spectrum can be destabilized by longer preferred PPMR or narrower feeding kernel (Law et al., 2009; Datta et al., 2011; Plank and

Box 2: Interaction kernels among individuals

Size-selective feeding kernel (Andersen and Beyer, 2006)
The kernel describes the preference of w_i-sized individuals to w_j-sized individuals:

$$\varphi(w_i/w_j) = \exp\left(-\left(\log\left(\frac{w_i}{\beta w_j}\right)\right)^2/(2\sigma_w^2)\right) \tag{4}$$

which is a lognormal function (Ursin, 1973), as graphed in Fig. 1. The function peaks when w_i/w_j equals the preferred predator-prey mass ratio β. Thus, individuals with mass ratio far from β are not able to interact. The range of prey size a predator exprience is determined by the width of the feeding kernel σ_w.

Remarks: This kernel is used in Paper II, III and IV. In Paper I, all consumer individuals prey upon the same unstructured resource. Thus, such feeding kernel is not assumed but the consumption rate remains size-dependent.

Spatial kernel (Hartvig, 2011)
The habitat trait in Paper I introduces a spatial kernel:

$$\psi(x_i - x_j) = \frac{1}{\sqrt{2\pi(\sigma_x^2(w_i) + \sigma_x^2(w_j))}} \exp\left(\frac{-(x_i - x_j)^2}{2(\sigma_x^2(w_i) + \sigma_x^2(w_j))}\right). \tag{5}$$

The spatial kernel assumes the abundance of individuals within a species N_i to be normally distributed in space with a center at x_i, and returns the strength of the interaction which is given by the spatial overlap of the interacting populations. The width of spatial distribution $\sigma_x(w_i)$ is the home range increasing with body size (Kramer and Chapman, 1999; Haskell et al., 2002; Jetz et al., 2004):

$$\sigma_x(w_i) = \sigma_0 + \frac{1}{2}\log_{10}(w_i/w_0), \tag{6}$$

where σ_0 is the home range of m_0 sized species.

Remarks: The spatial and feeding kernels jointly determines the interaction coefficients (i.e. α_{ij}) presented in equation (1) in Box 1.

Interference kernel
The modelling of interference competition in Paper IV introduces two kernels:

$$I_w(w/w') = \exp(-\log^2(w/w')/(2\sigma_w^2)), \tag{7}$$
$$I_m(m/m') = \exp(-\log^2(m/m')/(2\sigma_m^2)). \tag{8}$$

Interference is assumed to occur when two similar individuals encounter one another. Here "similar" means that the two individuals have similar body size (w) and similar trait value (m), described by a size interference kernel (7) and a trait interference kernel (8). The two kernels are Guassian-shaped with width governed by σ_w and σ_m, respectively.

Law, 2011). Viewed from evolutionary perspective, Weitz and Levin (2006) found an invariant preferred PPMR for given prey of a fixed size based on a scaled version of the Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963), and Loeuille and Loreau (2005) displayed that larger preferred PPMR and smaller width of feeding kernel tend to give rise to clearly distinct trophic levels. Via gradual evolution and successive speciation, wider feeding kernel promotes the emergence of large food webs with higher trophic levels (Brännström et al., 2010).

It is worth pointing out that, in aquatic ecosystems, the size-dependent predation produces individual ontogenetic trophic niche shift (Werner and Gilliam, 1984). As they grow bigger and bigger, individuals may change their trophic role from prey to predator. Thus, Jennings et al. (2001) argued that body size is a more appropriate measure of trophic level as apposed to species, and Jennings and Mackinson (2003) further found that the maximum food-chain length is negatively correlated with the preferred PPMR.

The three community models in Paper II, III and IV employ such size-dependent predation using a feeding kernel with fixed preferred PPMR and constant width. Differing from Paper III and IV in which predation is entirely size-based, an additional trait representing spatial distribution is added in Paper II, which together with body size determines the strength of predation interaction (equation (5) in Box 2). Since there is only one size-structured consumer and one unstructured resource in Paper I and cannibalistic interaction is not allowed, it is assumed that all consumer individuals can eat resource, the rate of which is, however, size-dependent.

Competition takes place in two different forms: exploitative competition which induces indirect negative effects on other species that share the same resources by reducing resource availability (Case and Gilpin, 1974; Vance, 1984), and interference competition which incurs direct effects by altering other species' ability of utilizing resource (Schoener, 1983; Vance, 1984). Both competition forms are ubiquitous in nature and interplay closely to affect population dynamics and community structure.

While exploitative competition is an indirect form arising from the use of a common resource, interference competition acts directly from a diversity of mechanisms across a wide range of species affiliation including aggressive behaviors (Walls, 1990; Kennedy and White, 1996), allelopathy (Rice, 1974; Harper, 1977; Nillson, 1994), overgrowth (Connell, 1961; Paine, 1966), and intraguild predation (Eaton, 1979; Leving and Franks, 1982; Ryti and Case, 1986; Polis et al., 1989). Furthermore, distinct interference mechanisms might induce disparately different effects on interacting species. The traditional definition of interference competition suggests that interference is costly. For example, each consumer species experiences a reduction in its per capita growth rate since the acts of interference reduce time and energy from resource exploitation, consequently leading to injury or death (Case and Gilpin, 1974; Schoener, 1983; Vance, 1984). However, for some mechanisms, interference could also be beneficial. Evidence is that aquatic invertebrates and fish tend to prey upon eggs and larvae that are their potential resource competitors (Polis et al., 1989). This intraguild predation can accrue the aggressor with increased per capita growth rate.

Interference competition has been studied heavily to understand species behaviors (e.g. Carothers and Jaksic, 1984; Briffa and Sneddon, 2007; Saito and Miki, 2010) and species coexistence (e.g. MacArthur and Levins, 1964; Armstrong and McGehee, 1976; Levins, 1979; Case and Casten, 1979; Tilman, 1982; Hochberg and Holt, 1990; Briggs, 1993; Kuang et al., 2003; Chesson and Kuang, 2008; Saito and Miki, 2010). Regarding species coexistence, general conclusion is that when negative intraspecific interactions are stronger than negative interspecific interactions, stable coexistence of competing species is favored. In contrast to these papers where only negative effects of interference were considered, Amarasekare (2002) investigated both costly and beneficial interference competition on species coexistence and found that if species engage in only costly interference mechanisms, they should not be able to coexist unless beneficial interference mechanisms are also engaged in. Interference competition has also been applied in the context of evolutionary speciation (Dieckmann and Doebeli, 1999; Doebeli and Dieckmann, 2000; Bürger et al., 2006), as interference is generally viewed as a major force driving natural selection (Diamond, 1978; Schoener, 1982). Results showed that interference competition is able to enable species evolutionary branching and emergence of complex food webs (Loeuille and Loreau, 2005; Brännström et al., 2010).

A common feature to the models mentioned above is that interference was simply represented as a single term (i.e. mortality), which contrasts sharply with its diverse mechanisms. The reason for this is mainly that the models were unstructured and parameterized at the species level, which makes different interference mechanisms mathematically indistinguishable. However, the constraints can be overcome using size-structured population model at the individual level. There are at least two advantages. One advantage is that interference interaction occurs directly among individuals rather than among species. Intra-specific interference competition can therefore be modeled explicitly. The other advantage is that using size-structured population model can formulate different interference mechanisms in a mathematically distinguished manner.

Inspired by these two advantages, Paper IV considers four interference mechanisms, i.e. reduction in the time on foraging, increase in maintenance costs, decline in the rates of survival and population recruitment based on the assumption that interference occurs when two similar individuals encounter one another. Here "similar" means that the two individuals have similar body size and similar trait value (equations (7) and (8) in Box 2). It is shown that different interference mechanisms results in distinct effects on the evolution of maturation size and the ultimate structure of emergent communities. Most importantly, only the last two types of interference competition favor the emergence of species-rich communities. In addition, once the interference competition is absent, leaving only the indirect exploitative competition and size-selective predation, only simple communities consisting of a couple of small species can appear. In the other three papers, only exploitative competition is considered.

2.2 Life history

Individual life history, comprising such as feeding rate, somatic growth, mortality rate, reproduction activity, and maintenance costs, act closely to govern the performance of individuals (de Roos et al., 2003) (e.g. Fig. 1). Consider fish organisms in aquatic ecosystems. Fish generally spawn millions of eggs as a strategy to compensate the extremely low survival rate of eggs (Durate and Alcaraz, 1989; Winemiller and Rose, 1993; Andersen et al., 2008). The successfully surviving individuals struggle to obtain food from the surroundings and try to avoid the uptake by other consumers. The consumed resource is distributed in some manner among individual life-history traits and utilized to stimulate the development of organismal organs. The fish individuals might have to experience several orders of magnitude in size before reaching maturation when reproduction occurs (Werner and Gilliam, 1984). Thus, over the course of the ontogenetic growth, many individual life-history processes undergo dramatic changes from birth to maturation, which undoubtedly affects individual ecological performance.

On the other hand, as dynamics and structure of populations and communities emerge actually as a product of the collection of the dynamics of individuals (Metz and Diekmann, 1986; Nisbet et al., 2010; Brännström et al., 2010; Hartvig et al., 2011), they are directly influenced by the ecological performance of individuals. For example, the juvenile delay between birth and the onset of reproduction tends to destabilize the system by exciting population cycles (Gurney and Nisbet, 1980), or small change in individual mortality may bring about catastrophic collapses to a community (de Roos and Persson, 2002). Conversely, the realized life history may be greatly affected by alterations in the processes of populations and communities, which affects the ambient food density on which an individual can forage. Therefore, individuals of similar age but being born at different times are likely to arrive at different size depending on the food experienced by individuals since birth (Claessen et al., 2000).

Thus, individual life history is not static but rather strongly correlated with population dynamics, and their intimate relationship calls for deep understanding of individual life-history processes when using individual-based model as a basis to predict the phenomena of populations and communities. To describe individual dynamics via individual life history, there are two key elements. The first is how to relate individual physiological states (e.g. size, age, length, reserves) with the rate at which individuals acquire resources from their environment, while the second is how to describe the way in which the absorbed energy is distributed among maintenance, growth and reproduction (Gurney et al., 1996). For many species, it is well documented that body size is one of the most important physiological state of an individual organism, and determines the type and strength of ecological interactions including the predation, exploitative and interference competition that are discussed above (Peters, 1983; Calder, 1984; Sebens, 1987; Werner, 1988; Werner and Gilliam, 1984; Brown et al., 2004). The size-dependent life-history processes have been demonstrated to be crucial for the demographic properties of populations and communities (for review see de Roos et al., 2003). The scaling of life-history

traits with body size is presented in Box 3.

Regarding the second element, Dynamic Energy Budget (DEB) theory (Kooijman, 2000, 2010; Nisbet et al., 2000; Sousa et al., 2008, 2010), describing the quantification of the energetics of individuals as it changes during life history, offers a compelling and systematic tool to deal with the issue of energy partition. The theory aims to relate some key life-history processes like feeding, digestion, storage, maintenance, growth, reproduction, product formation, respiration and aging to individual physiology obeying a set of simply mechanistically inspired rules for the uptake and use of substrates by individuals. As the DEB theory emphasizes on metabolic processes that are common to organisms of broad taxa, the tool is not constrained to individual affiliation and therefore possesses a high generality. A variety of DEB-based models have been developed and used for applications in population ecology (Lika and Nisbet, 2000; Pecquerie et al., 2009; Muller et al., 2009; Hall et al., 2009; Nisbet et al., 2010; Poggiale et al., 2010), toxicology (Lassiter and Hallam, 1988; Hallam et al, 1989; Kooijman and Haren, 1990; Kooijman and Bedaux, 1996) and biotechnology (Ratsak et al., 1993, 1996), organismal aging (van Leeuwen et al., 2010), subcellular metabolic network (Vinga et al., 2010).

Most DEB models in the literature can be classified into two classes, which are referred to as net-assimilation and net-reproduction models (Kooijman, 1993; Nisbet et al., 1996; Gurney and Nisbet, 1998; Noonburg et al., 1998; Lika and Nisbet, 2000; Nisbet et al., 2010), respectively. The two families of models differ mainly in the hypothesis concerning the way in which ingested energy is channeled to reproduction. The difference is schematically illustrated in Fig. 4. Clearly, the net-reproduction model assumes that the absorbed energy first meets the demand of maintenance with a top priority. Of the remaining energy, a certain part is utilized by growth and the other part by reproduction, the so-called κ-rule (Kooijman, 2000). In contrast, the net-assimilation models assume that part of the ingested resource is rooted to reproduction while the remaining to maintenance and growth. Although there is marked difference between the two mechanisms of energy distribution, there is no consensus on which mechanism of energy partition is dominate. Nisbet et al. (1996) found that different hypotheses of energy allocation may strongly affect prediction on toxicant response. Gurney et al. (1996) demonstrated that population-level behavior varies with energy allocation strategy.

Concerning size-structured population models for aquatic ecosystems, the two strategies of energy allocation among individual life history can be seen in many studies. On the one hand, regarding the net-assimilation strategy, de Roos et al. (1990) identified the prey-escape mechanism that underlies large amplitude consumer-resource cycles; Claessen et al. (2000) studied the effects of population feedback on individual life history; de Roos and Persson (2002) found that size-dependence in life history exerts an Allee effects; Claessen et al. (2004) investigated the cannibalism induced bistability. On the other hand, using the net-reproduction strategy, Andersen and Beyer (2006) derived the exponent of marine size spectrum using a trait-based size-spectrum model; Andersen and Pedersen (2010) explored fishing induced trophic cascade in marine communities; Hartvig et al. (2011) proposed a generic food-web

Box 3: Scaling of life-history processes with body size

Consumption rate

$$v(w) = \gamma w^q, \tag{9}$$

Encountered food

$$E(w) = v(w) \int w' N_c(w') \varphi(w/w') dw', \tag{10}$$

Maximum consumption rate

$$I_{max}(w) = h w^n, \tag{11}$$

Feeding level

$$F(w) = E(w)/(E(w) + I_{max}(w)), \tag{12}$$

Assimilated food

$$S(w) = \alpha I_{max}(w) F(w), \tag{13}$$

Maintenance cost

$$C(w) = k_s w^p, \tag{14}$$

Allocation function

$$\psi(w, M_j) = (1 + (w/(\eta M_j))^{-u})^{-1} (w/M_j)^{1-n}, \tag{15}$$

Somatic growth

$$g_j(w) = \max\{0, (1 - \psi(w, M_j))(S(w) - C(w))\}, \tag{16}$$

Birth rate

$$b_j(w) = \max\{0, \psi(w, M_j)(S(w) - C(w))\}, \tag{17}$$

Predation mortality

$$\mu_p(w) = \int v(w')(1 - F(w')) N_c(w') \varphi(w'/w) dw', \tag{18}$$

Starvation mortality

$$\mu_s(w) = \max\{(S(w) - C(w))/\xi w, 0\}, \tag{19}$$

Background mortality

$$\mu_b(w, M_j) = \mu_0 M_j^{1-n}, \tag{20}$$

Box 3: continued

where w is individual body size, M_j is the maximum body size of species j, and $N(w, M_j)$ is the size spectrum of species M_j (e.g. Fig. 3B). $N_c(w) = \sum_j N(w, M_j)$. $\varphi(w/w')$ is given by equation (4). Detailed description of such scaling and involved parameters refer to Hartvig et al. (2011) and Paper IV. Brief description of the life-history scaling goes as follows.

Predation provides individuals with food from resource organisms and other consumer individuals based on the size selection (4). The encountered food (10), proportional to the encounter rate of volumetric search which is increasingly dependent on body size (9), determines individual feeding level (12) in relation to the maximum consumption rate (11). With an assimilation efficiency α (13), aborbed energy is in priority used for standard metabolism (14) and then, if there is any, used for individual somatic growth (16) and reproduction (17) between which energy distribution is described by an allocation function (15). The growth equation indicates that the surplus energy after paying metabolic cost is entirely used for juvenile growth but drops due to the onset of reproduction. Growth ceases when individuals reach the maximum body size and all energy is routed to reproduction activity.

Besides the predation mortality (18), individuals also suffer from natural death that is trait-dependent (20) and starvation (19) when digested food is insufficient to meet metabolic costs. Thus, the total mortality that an consumer w-sized individual experiences is $\mu(w) = \mu_p(w) + \mu_b + \mu_s(w)$. Moreover, in case of starvation, growth and reproduction stop instantaneously. The adding of background mortality to system is to avoid unlimited growth in abundance of the largest individuals since they do not experience any predation.

Population dynamics is described using the McKendrick-von Foerster equation (2). The total reproduced offspring is recruited to species to form the lower boundary condition of the size spectrum (3).

framework that was designed in particular for the communities with size-structured populations. Strictly speaking, in the latter case, the allocation of energy between growth and reproduction is not the standard κ-rule but rather an extension by allowing the fraction of the energy channeled to growth to vary with individual size (Hartvig et al., 2011), which is referred to as the size-dependent net-production model of energy allocation (Fig. 4).

The idea behind the extended net-reproduction model is as follows. For immature individuals all surplus energy after paying metabolic costs is routed to individual somatic growth. When individuals mature reproduction takes place, a certain proportion of the net energy is channeled to reproduction activity, and the growth of

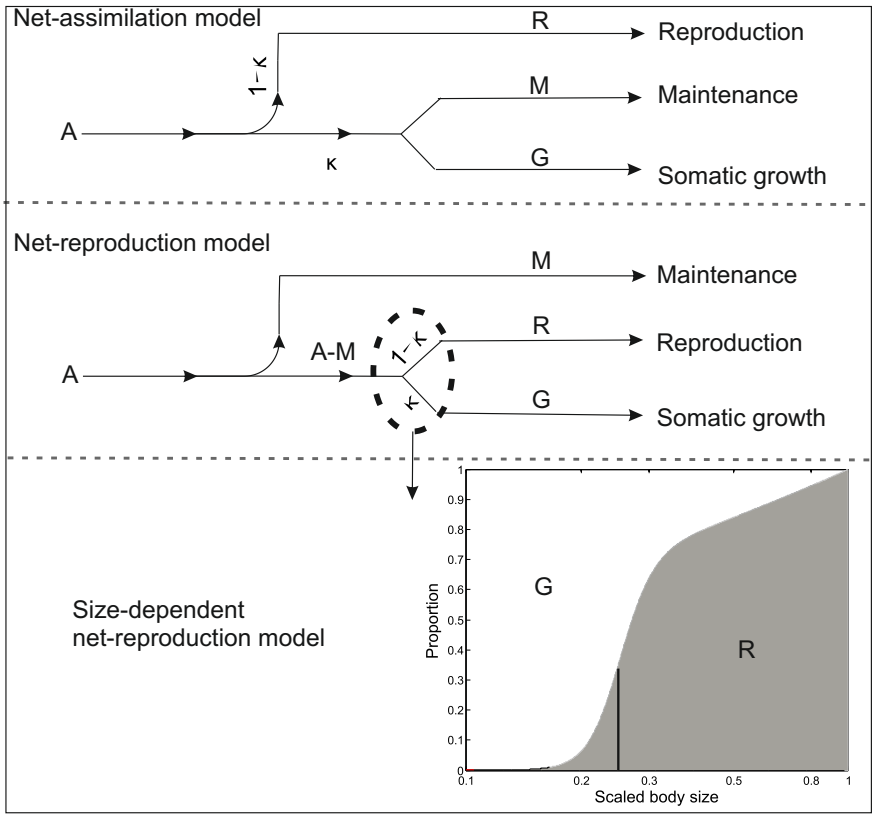

Fig. 4: Schematic representation of the three energy distribution in size-structured population model. The labels mean assimilated food (A), maintenance costs (M), somatic growth (G), and reproduction (R). κ indicates the fraction of energy that is consumed by some life processes. In the figure at the bottom, the y-axis shows the proportion $\kappa(w)$ of energy that is routed to reproduction, which is as a function of body size. Body size is scaled with maximum body size and the vertical dotted line indicates the scaled maturation size. Clearly, reproduction takes place a little bit early to account for other factors that lead individuals to reproduce before maturation. Nevertheless, their contribution to total reproduction is small. As individual grows bigger and bigger more and more energy is routed to reproduction. The size-dependent net-reproduction mechanism of energy allocation in this thesis is described by an allocation function (equation (15)). Assimilated food (A) is formulated by equation (13). Maintenance (M) is formulated by equation (14) and somatic growth (G) is given by equation (16). Reproduction (R) corresponds to the birth rate (equation (17)). At population level, the recruitment of offspring is described by equation (3).

individuals slows down. As individuals grow bigger and bigger, the proportion increases. When individuals approach the maximum body size, growth ceases and the surplus energy is all utilized by reproduction. Given the widespread consensus on the significant role of size-dependent life-history traits on the structure and dynamics of populations and communities (de Roos et al., 2003), it appears quite necessary to examine how the two different energy allocation strategies, i.e. net-assimilation and extended net-reproduction strategy, affect the predictions of the size-dependent life history as it is very likely that predictions from one hypothesis of energy allocation mechanism may be inconsistent with predictions from others (Gurney et al., 1996). Paper I conducts the comparison between two energetic hypotheses using a size-structured population model. The extended net-reproduction mechanism is also used in the models in Paper III and IV.

3 Scaling from individuals to the level of population

Scaling up from individual-level processes to the population-level dynamics is nontrivial and requires thorough considerations. Although all models in this thesis are individual-based, they differ in several aspects such as whether populations are structured, the level at which models are parameterized (single species or community as a whole), and whether they are food-web or size-spectrum oriented. Thus, various modelling approaches have been proposed.

3.1 Unstructured population models

The simplest approach of describing population dynamics is the classic Lokta-Volterra models (Lotka, 1925; Volterra, 1926) (equation (1) in Box 1). Such models can be extended in many directions, and very often the interaction coefficients are replaced with nonlinear functions such as the Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963) where a functional response describing the upper limit of the per capita consumption of prey species was incorporated.

Applying the traditional population models of Lotka-Volterra type to species-rich communities is challenging. The marked difficulty is to estimate the species-dependent parameters appearing in equation (1) (Box 1), which is not so tough for a few species, but becomes highly implausible with a surfeit of parameters as a result of rapidly increasing number of interacting species. To overcome this problem, Yodzis and Innes (1992) extended the Lotka-Volterra models to consumer-resource models on the basis of energetic reasoning and allometric empiricism. The idea is to assign each population a body size as a characteristic and relate parameters with body size and metabolic categories of the species in question. This bioenergetic approach makes the consumer-resource models capable of handling numerous species for the systems where body size governs most of life processes.

To summarize, the characterization of populations by body size and the allometric scaling of metabolism make the consumer-resource models in Yodzis and Innes (1992) generic. The generality allows such models to serve as building blocks with which food-web models can be developed and parameterized coherently across multiple species in particular at the individual level (e.g. Loeuille and Loreau, 2005; Brose et al., 2006a; Loeuille and Loreau, 2006; Lewis and Law, 2007; Brännström et al., 2010). The consumer-resource models can be tailored for particular research questions by taking more characteristics of populations into account such as foraging ability (Kondoh, 2003), vulnerability (Rossberg et al., 2008), habitat location (Hartvig, 2011) in addition to body size. The model in Paper II is built on the consumer-resource models of Yodzis and Innes (1992) but populations are represented by two traits: body size and habitat location. The two traits co-occur to determine the interaction strength and ultimately shape the structure of emergent food webs (equations (4) and (5) in Box 2; Fig. 2).

The obvious disadvantage of unstructured population models is the drastic simplification of the life history of individual organisms. For instance, reproduction of offspring is an instantaneous consequence of predation, which is not the case in nature. The weakness is due to the aggregation of individuals within populations, which ignores individual life history. To account for individual life history, structured population models are developed.

3.2 Structured population models for single species

Structured population models are generally motivated by the evidence of the remarkable intra-species size variability, initiated by individual growing during their life cycle (e.g. Fig. 1). In aquatic ecosystems, this feature is strikingly pronounced. For example, an adult cod could weight around 10 kg while its offspring larvae weights only around 0.5 milligram. The huge difference between adult cod and larvae cod suggests that this larvae cod has to grow over 5 orders of magnitude in size before maturation, a journey in which this individual cod changes diet and habitat (ontogenetic niche shifts) and accordingly the trophic role from prey to predator (Werner and Gilliam, 1984). The intra-species size variability has been increasingly recognized to have strong effects on population dynamics (Werner and Gilliam, 1984; Neill, 1988; Persson, 1988; Werner, 1988; Wilbur, 1988; Polis et al., 1989; Orr et al., 1990; Olson et al., 1995; Perrson et al., 1998; Claessen et al., 2000; de Roos and Persson, 2001). A remarkable effect is the cannibalism-induced alternative steady state (Botsford, 1981; Fisher, 1987; Cushing, 1991, 1992; Claessen and de Roos, 2003; Hartvig and Andersen, 2011), which enables a cannibalistic population to persist under the food conditions which cause the population to go extinct if cannibalism is absent, the so-called life-boat mechanism (van den Bosch et al., 1988; Henson, 1997). For a review of the cannibalism-induced impacts on population dynamics, one can refer to Claessen et al. (2004).

To account for physiological difference of individuals within a population, structured population models are formulated mathematically in several ways. The stage-

structured population model (Gurney and Nisbet, 1980; Lawton and Hassell, 1981; Gurney et al., 1983; Nisbet and Gurney, 1983; Gurney and Nisbet, 1985; Bellows and Hassell, 1988) simply separates individual life history into discrete stages e.g. juvenile and adult, which are linked through reproduction and recruitment. Individuals in distinct stages differ in, for instance, foraging ability and metabolic rates, thus leading to asymmetrical competition (Persson, 1985; Hamrin and Persson, 1986; Werner, 1994) when competing for resource. A common situation in a multi-trophic community is that large stage of top predator is affected positively by feeding upon small species whereas lower stage is affected negatively by its competition (Mittelbach and Osenberg, 1993; Olson et al., 1995). The indirect coupling of one stage to the dynamics of resource used by other life stages might be related to the competitive juvenile bottlenecks, a phenomenon that during the juvenile stage, a predator species may suffer from superior competition by a species that it later in life will prey upon (Persson and Greenberg, 1990; Persson et al., 1996).

The stage-structured population models aid understanding of individual interactions and their resulting population-level patterns. McCauley et al. (1999, 2008) employed a stage-based model to describe the population of Daphnia and identified a small- and a large-amplitude cycle in Daphnia-algal system. Nisbet et al. (2010) examined the effects of dynamic energy budget (Kooijman, 2000, 2010) on staged-structured Daphnia dynamics. However, stage-structured population models are especially appropriated for organisms with marked inter-stage difference but with slight intra-stage differentiation.

In contrast to the stage-structured population models, physiologically structured population models (PSPMs) do not require any subdivision of individual life stage but allows it to vary continuously against some physiological states e.g. body size (see Fig. 1) or age, (Metz and Diekmann, 1986; Metz et al., 1988; de Roos et al., 1990, 1992, 1997; de Roos and Persson, 2001). PSPMs primarily aim to describe the size-dependent interactions and establish an explicit link between individual-level performance and population dynamics. These models relate all relevant life-history processes (feeding, growth, mortality, reproduction) to individual physiological state and its biotic and abiotic environment, and assume a strict separation of individual interactions from population dynamics. The essential aspect of formulating PSPMs is to mathematically describe how the environment affects individual performance and how the individual in turn influences the environment. Thus all interactions are parameterized only at the individual level as opposed to the population level.

Population-level properties arise as emergent phenomena via bookkeeping of individual numbers as a function of individual state (de Roos and Persson, 2001; Diekmann and Metz, 2010), e.g. the abundance distribution as a function of body size (the bold curve in Fig. 1). The individual state is described deterministically by following the development of cohorts through a set of ordinary differential equations, and population dynamics can be described using the McKendrick-von Foerster equation. PSPMs have been applied in many situations (de Roos et al., 1990; Claessen et al., 2000, 2004; Claessen and Dieckmann, 2002; de Roos and Persson, 2002; de Roos et al., 2003; Persson et al., 2004; de Roos et al., 2010).

A logic link between the PSPMs and stage-structured population models can be established in some cases. In a consumer-resource system where consumer is size-structured while resource is unstructured, de Roos et al. (2008) demonstrated that the stage-structured models could be reduced from the PSPMs in the absence of cannibalism. In this case, the stage-structured model truely mirrors the PSPMs under both equilibrium and non-equilibrium conditions. However, the situation changes qualitatively when cannibalism is present. In the latter case, the stage-structure model fails to describe the dynamics due to the time delay it takes for an individual organism to grow from birth to maturation. It was concluded by de Roos and Persson (2001) that PSPMs offer a much higher degree of realism, precision and testing ability than lumped stage-based or unstructured models.

A variant of the PSPMs is the age-structured population models (Diekmann et al., 1986; Hastings, 1987; Cushing, 1994, 1998) when envisaging age to be one of individual physiological states. While age-structured model may work well for cohorts of animals or plants due to their synchronous developments through consecutive life stages, it may be inappropriate for other organisms to which the age is poorly correlated with individual life-history performance. For example, the growth rate of members of a single age-cohort can vary enormously from one individual to the next because of generic or environmental differences (Horn, 1979; Hughes, 1984).

Recall the profound influences of body size on individual life-history processes (de Roos et al., 2003), body size is an ideal option to characterize individual physiological state, which gives rise to the size-structured population models (Fig. 1, Box 1,2 and 3). This type of structured population models describes the density distribution as a function of individual body size by resolving individual life history. Paper I employs a structured population model of such type to investigate the impacts of different energy distribution among individual life-history processes on population dynamics (Fig. 4).

To summarize, the PSPMs could in principle be perceived as the basic framework to account for physiological variability among individuals. In this context, the stage-structured models are actually discrete versions of the PSPMs in physiology. Age- and size-structured population models are two specific cases of PSPMs, when age and size are, respectively, selected as the physiological state of individuals. While permitting highly realistic predictions on population dynamics through a limited set of mechanisms, PSPMs typically rely on large species-dependent parameter sets and cannot handle the dynamics of complex communities with large number of structured populations such as marine ecosystems (Hartvig et al., 2011). To describe the dynamics of such complex communities, there are two approaches: size-spectrum community models and food-web community models.

3.3 Food-web community models

There are in principle three classes of food-web models: topological, top-down population dynamical, and bottom-up population dynamical food-web models (Table 1).

In the first class, topological food-web approach consists of random model, cas-

Table 1: Food-web models

Model	Feature	Source
Topological models		
Random model	Any link among species occurs with the same probability equal to a given connectance.	Cohen et al. (1990); Solow and Beet (1998)
Cascade model	Assign each species a niche value uniformly drawn from the interval $[0, 1]$ and assume that a consumer eats all species with niche value smaller than itself.	Cohen et al. (1990)
Niche model	Similar to the cascade model but assume that a consumer eats all species with niche values falling into a range whose center is chosen randomly but smaller than the niche value of the consumer.	Williams and Martinez (2000)
Nested-hierarchy model	Each species is assigned a randmonly drawn niche value from $[0, 1]$, and the links among species are established according to their phylogeny and adaption.	Cattin et al. (2004)
Matching model	Topologies of food webs are designed based on the degree of correspondence between consumer and resource traits.	Rossberg et al. (2006)
Generalized niche model	Extend the niche model to high dimensional niche space.	Stouffer et al. (2005) Allesina et al. (2008)
Top-down population dynamical models		
	Combination of topological food-web models with population dynamics.	Kondoh (2003) Martinez et al. (2006) Brose et al. (2006a) Williams (2008)
Bottom-up population dynamical models		
Species-assembly model	Communities assemble themselves gradually as species migrate infrequently from a species pool either sequentially or simultaneously.	Drake (1990) Law (1999) Rossberg et al. (2008) Hartvig et al. (2011)
Species-speciation model	Communities arise as a consequence of population dynamics described by ecological interactions and adaptive dynamics governed by the processes of evolution and mutation.	Caldarelli et al. (1998) Drossel et al. (2001) Loeuille and Loreau (2005) Rossberg et al. (2008) Brännström et al. (2010)

cade model, niche model, nested-hierarchy model, matching model, and the generalized niche model. The key feature of each model is summarized in Table 1. The random model (Cohen et al., 1990; Solow and Beet, 1998) creates feeding links among a prescribed number of species with a fixed probability that equals the predetermined connectance. This creation of food webs encapsulates as much freedom as possible to maintain the pre-determined species diversity and connectance, whereas the assumption that species can consume each other with an equal probability seems highly unrealistic. The cascade model (Cohen et al., 1990), similar to the random model, assigns each species a value that is chosen at random from the interval [0, 1], and assumes that each species can only been eaten by the ones with values larger than itself. While succeeding explaining one aspect of food webs like species richness, the model fails to account for other aspects like food-chain length and interspecific trophic similarity. Extended from the cascade model, the niche model (Williams and Martinez, 2000) relaxes the cascade hierarchy of feeding links by restricting species to consume prey with niche values around the consumer's. In contrast to the random and cascade models, the niche model successfully demonstrates the main structure properties of the complex real food webs such as the distribution of species at top, intermediate and basal trophic levels, the means and variabilities of generality, vulnerability and food-chain length.

The nest-hierarchy model (Cattin et al., 2004) does not relay on one-dimensional niche space, but emphasizes groups of species and takes into account phylogeny and adaption implicitly. Species' diet is thought of as a consequence of the processes of phylogeny and adaption, which results in the diet discontinuity, a key difference from the diet contiguity in the niche model. The matching model (Rossberg et al., 2006) describes the evolution of an abstract species pool, which was considered to be the main mechanism structuring food webs. Such a model designs food-web topologies on the basis of the degree of correspondence between consumer traits and resource traits, and the evolution of traits of species is simply governed by random, uncorrelated speciation and extinction. The generalized niche model extends the niche model to be able to address multidimensional niches. The extension can be carried out either by introducing diet discontinuity to predator (Allesina et al., 2008), or by introducing "satellite prey" outside niche ranges (Stouffer et al., 2005). In contrast to the latter approach, the former can reproduce all the links in the empirical food webs (Allesina et al., 2008).

Although the topological models help the understanding of food-web properties, dynamical properties of food webs are completely absent in these models. Coupling of structure with dynamics might be necessary because population dynamics has profound effects on ecological architectures (Lewis and Law, 2007). The second class of food-web models incorporates population dynamics into the structural food-web models explicitly. The common feature of the topological and top-down population dynamical models is to use some aspects of community properties such as diversity and connectance to explain other aspects. This feature is, however, not appreciated because food-web structure is recognized to arise from the ecological interactions of individual species. Thus, there is increasing awareness of the importance of linking

community-level properties to species-level properties (Loeuille and Loreau, 2005; Brännström et al., 2010; Hartvig et al., 2011).

The bottom-up population dynamical models reconcile species-level properties with emergent community-level properties. They are comprised of two families: species-assembly models and species-speciation models. The two types of model assume that food-web communities do not appear in a single step but assembly themselves gradually in some ways. The former type of models (Post and Pimm, 1983; Drake, 1990; Law and Morton, 1996; Morton and Law, 1997; Virgo et al., 2006; Hartvig et al., 2011) describes an infrequent immigration of new species from a species pool that has already been determined priori to assembly. When chosen from the species pool, new species either is stably added to the community or fails to survive, of which both cases might be accompanied with extinctions of other species that exist before species' addition. Through addition and extinction, community composition is continuously shaped (see Fig. 2). Paper I adopts this approach to examine the relationship between food-web and size-spectrum representations of communities. Certainly, both the structure of species pools and the order of introducing new species will affect the ultimate outcome of communities.

While able to describe the emergence of food webs through the migration of species, the species-assembly models do not in general provide an adequate description of the origin of food webs because the structure and functions of obtained food webs are subjected to the architecture of the species pools. Quite differently, the species-speciation models, coupling evolutionary processes (Dieckmann and Law, 1996) with the population dynamics, do not incorporate the concept of species pools and species originate from speciation (Geritz et al., 1998), an evolutionary event entirely determined by the ecological interactions among species within communities (genetic speciation is not included here) (see Fig. 3A).

As a pioneer of the species-speciation models, the webworld model (Caldarelli et al., 1998; Drossel et al., 2001; McKane, 2004) depicts the evolutionary assembly of food webs using dozens of traits to represent species. It suggests that complex food webs might arise from evolutionary assembly process. However, the multiple traits make it difficult to test model predictions by using real data since the traits are not explicitly identified. Loeuille and Loreau (2005) employed a single well-identified trait, body size, to do evolutionary assembly and showed that rich food webs can be generated via simple ecological and evolutionary processes. The merit of this model is that using body size as a characteristic of species establishes an explicit link of some physiologically important aspects to food-web evolution. Thus, model predictions are more testable and applicable. The model was extended by Brännström et al. (2010) by incorporating gradual evolution (Dieckmann and Law, 1996) and evolutionary branching (Geritz et al., 1998) to mimic the emergence of food webs through small mutational steps. With the stimulated food webs, they explored the relationship between the initial diversification and the eventual diversification of evolved food webs and found that positive relationship is not always observed and additionally the most diverse food webs often do not have the highest trophic levels.

There are also some other species-speciation models. Tokita and Yasutmi (2003)

developed an evolutionary model with replicator equations (Hofbauer and Sigmund, 1988) to generate complex and stable food webs, whereas it is the interaction strengths rather than the underlying ecological traits that evolve in the model. Similar model was also used by Ackland and Gallagher (2004). Ito and Ikegami (2006) described the evolutionary dynamics in a reaction-diffusion model using two abstract traits in reflection of the roles of species in the two-dimensional phenotype space as prey and as predator. A complex food web appeared through recursive evolutionary branching from a single phenotypic cluster. Rossberg et al. (2008) proposed an allometric multitrophic model by employing multiple traits like body size, abstract foraging and vulnerability traits. The allometric scaling of abstract traits with body size made it possible for the model to yield realistic food webs through evolutionary processes of speciation, invasion and extinction.

Although promising, all of above models aggregate individuals and overlook the potentially significant effects of physiological variation among individuals with the same species. By synthesizing the PSPMs with the traditional food-web models, allometric body size scaling and trait-based modelling, Hartvig et al. (2011) developed a food-web model with size-structured populations at the individual level, where populations characterized by a trait: size at maturation. The size-structured food-web models can be viewed as a dynamical version of the trait-based size-spectrum model in Andersen and Beyer (2006) by modelling reproduction dynamically. Since parameter values were determined from cross-species analysis of fish communities, such model serves as a generic food-web framework for communities with structured populations (Andersen et al., 2008; Andersen and Pedersen, 2010; Hartvig, 2011). Paper IV incorporates the evolutionary process as used in Brännström et al. (2010) to this size-structured food-web model (Hartvig et al., 2011) and explores under what conditions food webs with size-structured populations can arise (see Fig. 3).

3.4 Size-spectrum community models

Using size spectrum to characterize marine ecosystems appears to be an appealing method to represent a complex community to a simple representation. The dynamics of marine size spectrum can be described deterministically with three distinct types of model at different levels: the community size-spectrum models (referred to as community models), the deterministic jump-growth (DJG) model, and the trait-based size-spectrum models (referred to as trait-based models). The three models are summarized in Box 4.

The community size-spectrum models describe the continuous biomass flow along the size spectrum from the smallest organisms to the largest ones with size-dependent growth and mortality. It is governed by the McKendrick-von Foerster (MvF) equation. The model was first derived by Silvert and Platt (1978), and further extended by Silvert and Platt (1980) to relate the growth at one size to death at another since large organisms prey upon small ones to grow. One constraint involved in their models is that a predator can only eat the prey of a fixed size, which is rather unlikely to hold in natural communities. Thus, Benoît and Rochet (2004) relaxed this

constraint by allowing a predator to consume prey organisms within a restricted size range, described by a feeding kernel (e.g. Fig. 1). Based on this model, Rochet and Benoît (2011) explored the impacts of fishing on marine size spectrum and found that size spectrum tends to be destabilized by fishing. Recently, Maury et al. (2007a,b) took more size-dependent processes and metabolic activities into account in the community model and examined the environmental effects on the dynamics of marine size spectrum.

Unlike the community models which assume an identical growth rate for all organisms of the same weight, the DJG model instead allows organisms, starting at the same weight, to grow to different weights as time proceeds forwards (Datta et al., 2010). In other words, when two organisms of the same weight encounter and feed upon prey organisms of different weights, they subsequently have different weights, potentially leading to jumps in their growth. The model is a macroscopic approximation of the stochastic jump-growth model that was derived on the basis of individual-based stochastic processes by Law et al. (2009). The approximation is effective when the system size is large, which is the right case in marine ecosystems. Datta et al. (2010) proved that the MvF equation is actually a first order approximation of the DJG equation. By comparing the stochastic jump-growth model, the DJG model, and the MvF equation, they demonstrated that the MvF equation is an appropriate approximation in equilibrium systems, but loses its accuracy in non-equilibrium dynamics, which can, however, be well described by the DJG model to a large extent.

The trait-based models take species identity into consideration, and describe the marine size spectrum indirectly via species size spectra (the abundance-body size relationship at the population level) (Andersen and Beyer, 2006). Community size spectrum is then the summation of all the size spectra of species that exist in the community. Species are characterized by a trait, maximum body size to which an individual within the species can attain. Thus, individuals are indicated by two indices: body size, representing their states, and trait, representing their taxonomical identity. Dynamics of species size spectra are governed by MvF equations and obtained by resolving individual life history. Importantly, predation is completely size-based whereas individual growth rate varies not only with body size but also with trait. Therefore, individuals of the same body size but belonging to different taxa will have different growth rates, leading to growth variation among individuals of the same size. Applying the trait-based model to fish communities, Andersen et al. (2009) studied the life-history constraints on the success of the many small eggs reproductive strategy and found that the success increases with the maximum body size until reaching a maximum and then decreases. Andersen and Pedersen (2010) examined the impacts of fishing on marine ecosystems and showed that fishing does not change the overall slope of the size spectrum, but depletes the largest individuals, and generates trophic cascades subsequently.

The community models and the DJG models describe the marine size spectrum at the ecosystem level and ignore species taxa which is explicitly included in the trait-based model. While the MvF equation proved to be the first order of the

Box 4: Modelling of marine size spectrum

Community size-spectrum model (Benoît and Rochet, 2004)

$$\frac{\partial}{\partial t}N(w) = -\int T(w',w)N(w)N(w')dw' - \frac{\partial}{\partial w}\int \alpha w' T(w,w')N(w)N(w')dw' - \mu N(w), \quad (21)$$

which is the McKendrick-von Foerster equation (McKendrick, 1926; von Foerster, 1959). Here, $N(w)$ describes marine size spectrum. The two integrals indicate predation mortality and growth in body size, respectively. μ is non-predation mortality. The function $T(w,w') = v(w)\varphi(w,w')$ is a feeding kernel of individual of size w on individual w' (see equations (4) in Box 2 and (9) in Box 3). α is the conversion efficiency of biomass from prey to predator.

Deterministic jump-growth model (Datta et al., 2010)

$$\frac{\partial}{\partial t}N(w) = \int (-T(w,w')N(w)N(w') - T(w',w)N(w')N(w) + T(w-\alpha w')N(w-\alpha w')N(w'))dw' - \mu N(w) \quad (22)$$

of which the first order approximation with respect to α is equation (21), and the second order approximation is

$$\frac{\partial}{\partial t}N(w) = -\int T(w',w)N(w)N(w')dw' - \frac{\partial}{\partial w}\int \alpha w' T(w,w')N(w)N(w')dw' + \frac{\partial^2}{\partial w^2}\int (\alpha w')^2 T(w,w')N(w)N(w')dw' - \mu N(w). \quad (23)$$

Remarks: Equation (22) stems from the stochastic jump-growth model developed by Law et al. (2009). In equation (23), the second order derivative is the diffusion of growth in body size, which has been demonstrated to stablize equilibrium solution (Datta et al., 2011; Plank and Law, 2011).

Trait-based size-spectrum model (Andersen and Beyer, 2006)

$$\frac{\partial}{\partial t}N(w,M) = -\int T(w,w')N(w,M)N_c(w')dw' - \mu N(w,M) - \frac{\partial}{\partial w}\int \varepsilon(w,M)w' T(w,w')N(w,M)N_c(w')dw', \quad (24)$$

where $N_c(w) = \int N(w,M)dM$, and M is the maximum body size, a trait characterizing species identity. $\varepsilon(w,M) = \epsilon(1-(w/M)^{1-n})$ is the individual growth efficiency.

Remarks: Individual production and maintenance are merged into the growth efficiency. $\varepsilon(w,M)$ results in asynchronous growth rate among individual of the same w but of different M (Andersen et al., 2009). Clearly, the mechanism responsible for the growth variability differs from the one in (23).

DJG equation (Datta et al., 2010), Andersen and Beyer (2006) demonstrated that the MvF equation can also be envisaged as an averaged version of the trait-based model by averaging individual growth rate over the trait. However, the growth variation is lost during the process of averaging. One implication is that predictions from community size-spectrum model might be unreliable, as growth variability has a stabilizing effect on the dynamics of size spectrum (Datta et al., 2011; Plank and Law, 2011). What should be kept in mind is that the mechanisms underlying the growth variability are different between the DJG model and the trait-based model. In the former model, the growth variability is a consequence of the inherent stochasticity in individual growth due to the random time to the next feeding event and the random size of the prey item eaten (Law et al., 2009). In the latter model, it results from the inclusion of species identity that leads deterministically to the distribution of growth rate among the individuals of the same body size but of different trait values (Andersen et al., 2009).

The three types of size-spectrum model are usually used to explain the size-spectrum patterns that are widely observed in natural marine communities (Silvert and Platt, 1980; Camacho and Solé, 2001; Benoît and Rochet, 2004; Law et al., 2009; Datta et al., 2010), and explore the consequences of fishing (Andersen and Pedersen, 2010; Rochet and Benoît, 2011). Paper III uses the trait-based size-spectrum model to explore the influence of the trait-induced growth variability on the stability and regularity of community dynamics. It is worth pointing out that none of these models are food-web frameworks. Although the trait-based model (Andersen and Beyer, 2006) includes species identity, the trait is continuously distributed. In addition, individual reproduction is not explicitly modeled and reproduction of offspring is assumed to be constant over time.

4 Community-level patterns

At the heart of community ecology is to explain the structure and dynamics of communities such as species diversity, stability, trophic-chain length, and size-distribution, for which the mechanisms accounting have not been well understood despite decades of intense efforts. Exploration for potential mechanisms requires an abstract representation of communities. There are in general two representations: food web and size spectrum, and different representations focus on different community properties. The thesis considers both representations. In this section, a brief description of community properties in relation to the work presented in this thesis is made for each community representation.

4.1 Food-web properties

Food web, the traditional community representation, emphasizes the taxonomic composition of communities. It reflects the trophic relationship and network diagram in which each node represents a species and each link connecting two nodes represents one species feeding on another (e.g. Fig. 5A). Food-web models have long been the

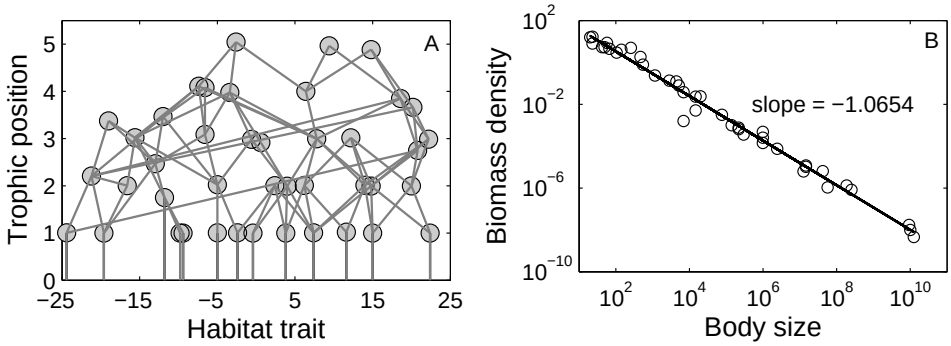

Fig. 5: Food-web (A) and size-spectrum representations (B) in correspondence to the assembled community in Fig. 2. Nodes represented species and are linked when a prey makes a contribution greater than 5% to the diet of its predator. The slope is the size-spectrum exponent, the key characterization of size-spectrum representation. Details of this figure refer to Paper II.

subject of extensive study in community ecology with a vast range of published literature. Among food-web properties, topics pertaining to species diversity, community stability, and food-chain length are extremely interesting to ecologists.

Species diversity, quantified by species richness in ecological communities, is receiving increasing attention due to the accelerating rate of biodiversity loss (Rickefs, 1987). With increasing awareness of the essential role of species diversity in ecosystem functioning (Rickefs, 1987; Naeem et al., 1994; Tilman, 1996; Loreau et al., 2002; Naeem and Li, 1997), it is necessary to understand the underlying processes responsible for emergence and maintenance of diversity in order to predict the consequences of change in system functions after deterioration. Viewed from ecological point of view, species richness is usually understood in the context of species coexistence (Chesson, 2000). Identifying what mechanisms promote species coexistence undoubtedly adds great help in maintaining the conservation of species diversity. In a recent review paper of Chesson (2000), various mechanisms enhancing species coexistence were listed, including predation, competition, habitat area, and resource availability (Chase et al., 2002; Kuang et al., 2003; Chesson and Kuang, 2008). Paper I demonstrates that energy partitioning among individual life-history processes is a factor, which constrains the coexistence of an size-structured consumer and an unstructured resource.

Viewed from evolutionary perspective, emergence of species diversity has been studied, for instance, by Loeuille and Loreau (2005) and Brännström et al. (2010) with bottom-up dynamical food-web models. Both papers concluded that species-rich communities can arise based on simple ecological and evolutionary rules. Paper IV extends these works from unstructured populations to size-structured populations and explores how different interference competition influences the evolutionary formation of large food webs. Results show that diverse community can be driven by interference competition through continuous evolutionary branching.

Stability of communities is very often linked to species diversity because of the

diversity-stability paradox that complexity destabilizes food webs theoretically, while the opposite seems always true in real ecological communities, which ignites the one of the most enduring debate in ecology. The paradox was recognized by May (1972) using a food-web model with randomly constructed interaction strengths, who claimed that there are no mathematical reasons to expect greater diversity enhancing community stability. This claim was latter criticized because the interaction strengths among interactions species are far from random but organized in some manners. Using plausible interaction strengths estimated from real data, Yodzis (1981) found that the resultant food webs are more stable than randomly constructed food webs, highlighting the crucial role of interaction strength in food-web stability. This finding was further reinforced by McCann et al. (1998), who demonstrated that weak links tend to stabilize communities. Real food webs also suggest that interaction strengths among interacting species are generally weak (McCann, 2000). To understand why weak links make community stable, Neutel et al. (2002) discovered that in real food webs, interaction strengths are organized in trophic loops in such a way that long loops consist of relatively many weak links. This link patten was mathematically displayed to reduce maximum loop weight and the amount of intraspecific interaction needed for matrix stability. In addition to link patterns, several other mechanisms were also identified as drivers of stability, including foraging adaption (Kondoh, 2003), asymmetry of community structure (Rooney et al., 2006), and the relationships between species body masses and feeding interactions (Otto et al., 2007). Most recently, two universal rules of promoting food-web stability were unraveled by Gross et al. (2009) that species at a high trophic level feed on multiple prey species on the one hand, and species at intermediate trophic level are fed upon by multiple predator species on the other.

A common feature of these stability analysis is the local stability of equilibrium solutions, determined by the Jacobian matrix corresponding to the ordinary differential equations that govern the dynamics of unstructured populations. The local analysis of equilibrium in unstructured population models motivates the study in Paper III with size-structured populations. Results show that trait diversity promotes the stability of community dynamics. Although the model in Paper III is not a food-web model, it can be compared to more traditional methods so directly as it helps to make sense of how trait diversity could help smooth out community dynamics by having more flexibility. This is an important contribution for the rapidly developing area of food webs with trait dynamics

However, the concept of stability is multifaceted, and different definitions of stability describe different properties of ecosystems (Ives and Carpenter, 2007). Paper II considers an community stability measured by the resistance to alien invasions. An impressive finding is that community stability is invariant with respect to the size of species pool. Stability is measured as the proportion of the areas with positive invasion fitness to the total trait space (Fig. 2). As species are characterized by traits which are continuous, the result implies that if species can be created in real world then all communities are equally invulnerable to alien invasion. Although this hypothesis is intuitively impractical, it might be arguably true to some extent,

viewed from the perspective of dispersal and mutation on the evolutionary time scale.

Food-chain length, the number of feeding links from a basal species to a top predator, is widely recognized as a key feature of food-web communities (Pimm and Lawton, 1977). Its profound effects on community structure (Carpenter and Kitchell, 1993), ecosystem functions (de Angelis, 1992), and contaminant concentrations in top predators (Cabana and Rasmussen, 1994) beg the question what determines food-chain length. Five hypotheses have been proposed since the recoganization by Elton (1927) that food-chain length varies among real communities, including (i) energy hypothesis (Lindemann, 1942) that resource availability limits food-chain length, (ii) dynamical stability hypothesis (Pimm and Lawton, 1977) that longer food chain rarely exists in fluctuating ecosystems, (iii) the optimal foraging hypothesis (Hastings and Conrad, 1979; Kondoh and Ninomiya, 2009) that the length of food chain is constrained by the optimal diet choices of individual species, (iv) design hypothesis (Pimm, 1982) that the constraint that a prey should be smaller than its predator limits food-chain length, (v) ecosystem-size hypothesis (Post et al., 2000) that food-chain length increases with ecosystem size (i.e. habitat area). These hypotheses act in concert to determine food-chain length, but the effect of each determinant may not be symmetrical for a given community and which exerts dominant impact depending on the targeted community (see also Paper II). For example, resource availability plays minor role in an ecosystem with rich resource availability (Jennings and Warr, 2003). Thus, Post (2002) suggested that it does not make sense to argue which determinant limits food-chain length but is more reasonable to explore when and where different determinants operate.

4.2 Size-spectrum properties

Size spectrum, disregarding species taxonomic affiliation, describes the density of organisms belonging to different body size classes (e.g. Fig. 5B). The concept of size spectrum was coined by Sheldon and Parsons (1967) as a method of organizing counts of particulate matter in the oceans, and later appeared as a new branch of community ecology to deal with the relationship between density and body size in both aquatic ecosystems (Sheldon et al., 1972; Sprules and Munawar, 1986; Ahrens and Peters, 1991; Cyr et al., 1997b) and terrestrial ecosystems (Peters and Wassenberg, 1983; Brown and Maurer, 1986; Cyr et al., 1997a). The approach has an advantage that it allows to examine quite complex ecosystems by using body size of individuals as the only trait.

Power-law relationship is frequently observed between the density and individual body size (Sheldon et al., 1972; Kerr, 1974; Boudreau and Dickkie, 1992; Quinones et al., 2003). The biological interpretation is that individual abundance decreases log-linearly with increasing body size, which can be formulated mathematically as $N(m) = N_0 m^{\lambda}$, where N_0 reflects the ecosystem differences in nutrient circulation and availability (Boudreau and Dickkie, 1992) and the exponent λ characterizes the size-spectrum pattern, which is in general negative. Cyr et al. (1997b) compared

the size spectrum between aquatic and terrestrial ecosystems and found that aquatic species are on average 6-60 times abundant than the terrestrial species. Rossberg et al. (2008) showed that the size-spectrum exponent λ is independent of the allometric scaling exponent of individual physiological rate and further the widely observed inverse abundance-size relationship could be explained by the top-down mechanism.

In marine ecosystems, the exponent is empirically predicted to be close to -1 on a logarithmical scale of abundance and of body size (Sheldon et al., 1972; Boudreau and Dickkie, 1992; Kerr and Dickie, 2001; Jennings and Mackinson, 2003). It is biologically interpreted as that small organisms are more abundant than large ones but their biomass is approximately invariant over logarithmically equal body size intervals. Theoretical studies further confirm this observation (Silvert and Platt, 1980; Camacho and Solé, 2001; Benoît and Rochet, 2004; Andersen and Beyer, 2006; Law et al., 2009). Besides, similar conclusions about size-spectrum exponent can also be made in species-rich model communities (Rossberg et al., 2008, Paper II). An important application of the size spectrum from the perspective of applied ecologists is that size spectrum can potentially serve as an indicator of human-induced impacts on marine ecosystems (Shin et al., 2005), fishing for instance (Rice and Gislason, 1996).

Stability of community size spectrum is generally restricted to marine ecosystems. Understanding of what determines the stability of marine size spectrum remains limited, but awareness of what makes marine ecosystems resilient or susceptible to biotic and abiotic factors is of paramount interest from both scientific and economic perspective in particular at a time of climate change and human-induced heavy exploitation of marine resource. As an example, consider the exploited fish stock. As fishing generally targets at large organisms, exploitation of large fish causes highly variability in size truncated populations (Hsieh et al., 2006; Andersen et al., 2008a), and thus can potentially induce a fundamental shift from one state to another (Knowlton, 2004) as documented in the post-exploited marine communities that were formerly dominated by cod (Frank et al., 2005).

The three types of size-spectrum community models (Box 4) all admit the power-law steady state. Stability analysis of the power-law steady state was first analytically made by Arino et al. (2004), who found that the size-based opportunistic predation could account for the stability in the shape of size spectrum, but predator growth is entirely size-dependent and not linked to prey density. Law et al. (2009) numerically discovered in a jump-growth model a new attractor in size-spectrum dynamics in addition to the power-law steady state. It is a traveling-wave solution which moves along the size spectrum from small to large body size. Moreover, the shift from the traveling wave to the power-law steady state is more likely to occur as predators prefer prey that is much smaller than themselves and when they are more specialized in the size range of consumed prey. Capitán and Delius (2010) investigated the stability of the power-law steady state in a scale-invariant model which is an extension of the jump-growth model by including the rates of density-independent processes like reproduction and maintenance, and demonstrated that the maintenance of respiration and reproduction has a strong stabilizing effect. A

systematical examination of the stability of the power-law steady state was performed analytically by Datta et al. (2011). They considered the power-law steady state of infinite length in the deterministic jump-growth model, of which the first order approximation is the McKendrick-von Foerster equation and the second order approximation is the McKendrick-von Foerster equation with a diffusion term in growth. It was found that the power-law steady state is more likely to be stable with smaller predator-prey mass ratio, larger diet width of predator, and higher feeding efficiency. These findings were confirmed once again in the numerical study by Plank and Law (2011), who employed the same model as Datta et al. (2011) but truncated the power-law steady state to a finite range. Importantly, these two papers both showed that the diffusion term in the second order approximation has a strong stabilizing effect in comparison with the McKendrick-von Foerster equation.

As the mechanism for the growth variability in the deterministic jump-growth model and its second order approximation is actually a demographic noise due to the discrete process of food consumption, and thus fundamentally different from the one introduced in the trait-based size-spectrum model (Andersen and Beyer, 2006; Andersen et al., 2009), it is natural to ask how the growth variability caused by the inclusion of trait affects the dynamics of marine size spectrum. Motivated by this question, Paper III explores the effects of trait-induced growth variability on the stability of equilibrium size spectrum as well as the dynamical properties of non-equilibrium solutions by comparing the trait-based size-spectrum model and the community size-spectrum model. It is shown that the introduction of trait diversity (accounting for the growth variability) makes the model communities more likely to be linearly stable, and if the community is unstable, the non-equilibrium dynamics has much smaller, slower, and more regular oscillations than if diversity is not taken into account. It is concluded that trait diversity helps smooth out community dynamics by having more flexibility.

Trophic level is investigated far less extensively with size-spectrum representations than with food-web representations. Size spectrum is motivated for representing marine ecosystems with numerous species and extremely complex trophic patterns. Specifying the trophic level of each species seems highly implausible. In addition, individual ontogenetic shift is another factor that impedes clarifying the relationship between size spectrum and trophic structure (Jennings et al., 2001; Hartvig, 2011, Paper IV). However, what is clear is that larger individuals are expected to feed up at higher tropic level, as body size determines the range of prey sizes a predator can eat (Cohen et al., 1993). Therefore, although body size is a poor surrogate of trophic level for individual species, it can be seen as an excellent indicator of trophic level for individual organism with community (Jennings et al., 2001). Nevertheless, the basic trophic feature in a community dominated by size-structured species can be described with the average trophic positions of adult individuals (Hartvig, 2011, Paper IV).

To summarize, food-web and size-spectrum are two widely used representations of ecological communities in ecological theory. As different ways of representing the same underlying community, they should be compatible in many aspects, although

they are historically studied separately. Paper II carries out this comparison and shows that there is a good correspondence between food-web and size-spectrum representations in particular for species-rich communities.

5 Conclusions

The thesis theoretically addresses several questions of interest to ecologists like individual life history (Paper I), food-web emergence (Paper II, IV), and community stability (Paper III), using various mathematical models. The mathematics to describe population dynamics differs qualitatively in whether populations are structured. Unstructured populations are modeled via a set of ordinary differential equations like the Lotka-Volterra equations (Lotka, 1925; Volterra, 1926) (Paper II), while continuously size-structured populations via a set of partial differential equations known as the McKendrick-von Foerster equations (McKendrick, 1926; von Foerster, 1959) (Paper I, III and IV). For models to capsulate a high realism of biology, most model parameters are scaled allometrically with body size that is widely considered to be an ideal indicator of modelling individual life processes (Peters, 1983; Woodward et al., 2005; Marquet et al., 2005). Moreover, interactions such as predation and competition in all models are individual-based instead of species-based because it is individuals rather than species that interact directly. The qualitative and quantitative relationship between differently sized individuals are defined by body size.

5.1 Contributions to ecological theory

The investigations in this thesis add several contributions to current ecological theory:

1. Growth curve plasticity has profound effects on population dynamics. Fast growth shortens juvenile delay between birth and the onset of reproduction, and thus makes the juvenile bottleneck more likely to be avoided (Paper I). Consequently, species are more likely to survive but population dynamics tends to be destabilized as a trade-off. Such kind of effect has been explained with, for instance, prey-escape mechanism (de Roos et al., 1990), size-selective foraging habit (de Roos and Persson, 2002), and competitiveness ability of differently sized individuals (de Roos et al., 2003). Here, we show that different mechanisms of energy partitioning can also exert similar effects.

2. The reconciliation of the food-web (Cohen et al., 1990) and size-spectrum (Sheldon et al., 1972) representations of communities bridges the two traditionally separately studied disciplines via traits (i.e. body size and habitat location) that are used as representatives of species (Norberg et al., 2001; Bruggeman et al., 2007; Merico et al., 2009, Paper II). Despite some discrepancies, the two community representations maintain a high coherence especially in terms of the exponent of individual size distribution. Linking trophic level to body size, the size-spectrum representation is able to capture the maximal trophic level

due to the energetic constraint (Lindemann, 1942). Other constraints like structure and ecosystem size (i.e. habitat area) (Cohen and Newman, 1991; Post et al., 2000) can only be displayed by the food-web representation.

3. The growth variability among individuals of the same size but belonging to different species is a stabilizing factor in complex community systems (Paper III). Looking back at the rich history of stability in ecology, one can immediately find many mechanisms of promoting community stability such as diversity which is supported empirically (Ives and Carpenter, 2007) although criticized theoretically to some extent (May, 1972), weak trophic interactions (McCann et al., 1998), patterning of links with long but low weighted loops (Neutel et al., 2002), foraging adaption (Kondoh, 2003), allometric degree distribution (Otto et al., 2007). Whereas the stabilizing effect of growth variation was noted previously by Datta et al. (2011) and Plank and Law (2011) in a jump-growth model, their mechanism accounting for the variation ascribes to stochastic events, differing radically from the deterministic mechanism arising from the inclusion of trait diversity in this thesis. Thus, the finding is an important contribution for the rapidly developing area of food webs with trait dynamics.

4. Four types of interference competition are mathematically formulated in a size-structured population model for the first time at the individual level according to their influences on the ecological performance of individual and population, including foraging, maintenance, mortality, and recruitment (Paper IV). The success of expressing the various interference forms attributes to the disaggregation of individuals within population and has a profound implication for two reasons. First, interference competition is ubiquitous in nature (Case and Gilpin, 1974), whereas traditional approach of modelling interference is merely a single term (mortality) in species-based population models. Ignoring the diversity of interference mechanism in unstructured population modelling is more likely to overlook some potential influences of interference as different interference mechanisms might have dramatically different effects on population dynamics, species diversity and ecosystem functioning. Second, interference competition is traditionally supposed to take negative effects by reducing population growth rate, although positive effects can in some cases be assumed (Amarasekare, 2002). In size-structured population models as in this thesis, such assumptions are not necessarily made *a priori* because population dynamics is a consequence of individual interactions. Combined with predation, the four interference forms may provide comprehensive understanding of the interplay between direct interactions at the individual level and phenomena at the community level.

5. The disparate evolutionary responses of species' size at maturation (Paper IV) enrich the theoretical understanding of the interplay between population feedback and individual life history. Their relationship has been investigated

extensively from the ecological point of view and a handful of conclusions are available (de Roos et al., 2003). Viewed from evolutionary perspective results are rather limited in the case of models with explicitly expressed individual life history in size-structured population models. Paper IV shows that size at maturation is either depressed or elevated depending on the underlying density-dependent interference competition, which represents the population feedback.

6. The emergence of complex food-web communities with structured populations through gradual evolution and successive evolutionary speciation enlightens our understanding of food webs from two aspects (Paper IV). First, food-web communities were traditionally approached evolutionarily with unstructured population models (e.g. Loeuille and Loreau, 2005; Rossberg et al., 2008; Brännström et al., 2010), although models may also be parameterized at the individual level. In the presence of individual life history our main results are consistent with the predictions from unstructured models, suggesting the robustness of the explanations of the observed community features like diversity and trophic level. Second, the patterns of stimulated food webs vary with interference mechanisms both qualitatively and quantitatively as different interference mechanisms cause distinct impacts on individual life history. Thus, explaining the structure of observed food webs should be correlated with the underlying interaction form.

5.2 Ecological perspectives

There are some suggestions and open questions for future study:

1. As seen from Paper I, different energy allocation strategies have disparate influences on population dynamics. A question arises naturally which strategy is prevailing among individuals. There is unfortunately no clear answer and both strategies are currently being used in literature (e.g. Kooijman, 2000; Lika and Nisbet, 2000; Claessen et al., 2004; Hartvig et al., 2011). Nonetheless, there is a tendency towards the net-production model as maintenance is increasingly recognized to have a top priority of utilizing energy (Lika and Nisbet, 2000). One message is, however, pretty clear that it is prudent to test the predictions from the employed energy allocation mechanism before using any model of individual life history to describe population dynamics.

2. An obvious limitation to the unstructured population model in paper II is the linear relationship between food consumption and per capita population growth rate. For most populations, there exists a maximum consumption rate constrained by the physiological capacity of individuals (Yodzis and Innes, 1992). Moreover, temperature has profound effects on individual metabolic costs and population growth (Gillooly et al., 2001, 2002; Savage et al., 2004). Thus, to test the robustness of the findings in this paper it is desirable to extend

the model by incorporating functional response and temperature-dependent metabolism.

3. Paper III reveals that trait diversity tends to stabilize equilibrium solutions and regulate the dynamics of non-equilibrium solutions by entitling communities more flexibility, but there is only one trait, i.e. maximum body size, is included. Adding additional traits (e.g. habitat location, vulnerability, foraging) might produce qualitatively similar effects because all traits will eventually work on individual somatic growth as argued in the paper. However, it is necessary and important to manifest the argument by incorporating directly one or more traits into the trait-based size-spectrum model (Andersen and Beyer, 2006).

4. Interference competition has been demonstrated to promote species coexistence and thus the reservation of biodiversity (Kuang et al., 2003) using unstructured population models, in particular when intraspecific interference competition is greater than interspecific interference competition (Saito and Miki, 2010). Given the four explicit forms of size-based interference competition in a trait (size at maturation) based size-structured population model (Paper IV), it remains an open question how they affect species diversity. Nonetheless, Hartvig et al. (2011) showed that large communities are hard to emerge through ecological community assembly unless additional traits (e.g. habitat trait or species preference) are included. In their model there is no direct interaction apart from predation. As shown by Chesson and Kuang (2008) competition and predation have equivalent potential to strengthen or weaken diversity maintenance, it is ecologically important to check whether species diversity can be enhanced in the presence of interference competition in the model of Hartvig et al. (2011).

5. Size-selective fishing alters the composition and dynamics of multi-trophic communities by removing large individuals that are commercially valuable (Andersen and Pedersen, 2010; Rochet and Benoît, 2011). As a consequence, density-dependent life history will be straightforwardly affected by these alterations. Few studies have shown that size-dependent mortality has substantial effects on life-history evolution (e.g. Heino and Kaitala, 1996; Conover and Munch, 2002; Taborsky et al., 2003; Law, 2007), but no population feedback was ever under consideration. Using the communities that obtained via coevolution and speciation in Paper IV, the evolutionary response of life-history traits towards fishing in multitrophic communities might be able to be examined systematically.

5.3 Mathematical challenges

Although receiving great help from computer technology, analyzing the models with many species and/or with size-structured populations is still mathematically challenging.

1. In Paper I, the method of reducing the system consisting of a PDE and an ODE to a system of coupled delay-differential equations is effective to determine the stability of equilibrium solutions. This method does not require any discretization of the range over which individual organisms span in size. Moreover, the size distribution of the consumer species is represented by an introduced population birth rate, which is a scalar (Diekmann and Metz, 2010). The obvious disadvantage of this method is that direct intra-population interaction (e.g. cannibalism) is not allowed, which limits this application considerably. It is mathematically interesting to extend this approach to include direct interactions within and across size-structured populations (de Roos et al., 2010).

2. An intriguing question pointed out in Paper II is what happens to the evolutionary steady state (ESS) as the dimension of trait space increases. The ESS is a community state in which no species with trait values other than the values of the existing species can invade the community (e.g. Fig. 2D). In one dimensional trait space, there exists a unique ESS that is reachable through community assembly. In two dimensional trait space, numerical examinations show that the composition of assembled communities undergo continuous changes. Probably, increasing the dimension of trait space will alter the nature of the evolutionary attractor contained in lower dimensional trait space. It remains unknown whether there are ESSs, and whether they are reachable by assembly, if there are any, in high dimensional trait space.

3. The study of nonlinear dynamics of the marine size spectrum (Paper III) concludes that the equilibrium solutions of the community size-spectrum model is seemingly a good approximation of the average of the non-equilibrium solutions of the trait-based size-spectrum model. This mathematical averaging property proves true in the classic Lotka-Volterra predator-prey models with periodic solutions (Hofbauer and Sigmund, 1988) and also valid for the almost-periodicity solutions to a more general class of bi-linear food-web models (Law and Morton, 1993). However, there is no theoretical reason to expect the averaging property to hold in the size-spectrum models as they do not have the bi-linear form of the Lotka-Volterra type. Thus, the conclusion is mathematically imprecise, but if it is true, a profound implication can be inferred directly that study on equilibrium can still provide valuable insights of community dynamics, even though communities are generally kept in a transient states owing to widespread disturbance (Pickett and White, 1985; Fukami and Nakajima, 2011). Hence, more rigorous tests are demanded.

5.4 Final remarks

Vellend (2010) concluded that in community ecology numerous ecological processes that underpin the observed community patterns can be in essence classified into four categories at the most general level: drift (stochastic changes in species abundance),

dispersal (movement of species across space), selection (deterministic fitness differences among species), and speciation (creation of species). The thesis covers the last three aspects. Predation and competition are only two of many factors determining species fitness. Assembling communities by choosing species from a predetermined species pool falls under dispersal. Emergence of species via mutation falls into the family of speciation. Three processes all take place at the individual level with body size linking them closely.

An important and interesting dimension that should be reinforced is the process of dispersal, because both ecological and evolutionary processes are influenced by individual distribution within habitat and between different geographic locations (Vellend, 2010). It has long been recognized that dispersal, being a life-history trait, has profound influences. Viewed from ecological perspective, dispersal affects population dynamics and persistence, species distribution, and thus community-level patterns (McCann et al., 2005; Amarsekare, 2008a,b; Eklöf, 2009). Viewed from evolutionary perspective, dispersal determines the level of gene flow between populations, and thus influences the processes including adaption, speciation and life-history evolution (Dieckmann and Doebeli, 1999). Moreover, in size-structured population models, an advantage is that the disaggregation of individuals with species allows to disentangle the differential ability of dispersal when individuals are characterized by body size. The size-dependent dispersal is more like to result in asynchronous spatial dynamics within species, which consequently shapes the spatial distribution of species and subsequently community structure. Therefore, a promising extension of the current works in this thesis is to get dispersal included to interplay with other life-history processes.

In conclusion, theoretical investigations via mathematical models reveal many new patterns and underlying mechanisms, and illuminate old ones. On the one hand, the deeper understanding of the ecology and evolution of populations and communities through more available field data and faster developed experiments fuels up the expansion of mathematical modelling considerably. To reflect the complexity of natural communities and capture the essential aspects of organisms, since the simplest Lotka-Volterra equations, mathematical modelling has been undergoing substantial changes both qualitatively (e.g. by incorporating life-history traits as done in paper IV) and quantitatively (e.g. by modelling a large number of interacting species as shown in paper II). On the other hand, mathematical models prove helpful in explaining observed community patterns, although predictions from different models that are tailored for the same ecosystem may differ. For instance, Paper I shows that the way in which energy allocation among life-history processes is one of many mechanisms that destabilize population dynamics, including the prey-escape mechanism (de Roos et al., 1990), juvenile competitiveness (de Roos et al., 2003). In addition, Paper III demonstrates that trait-induced growth variability tends to stabilize marine size spectrum. Whereas similar effect was also detected in the deterministic jump-growth model (Datta et al., 2011; Plank and Law, 2011), the mechanisms responsible for the growth variability is fundamentally different. These findings alarmingly highlight the importance of assumptions lying behind mathe-

matical modelling.

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Summary of papers

Paper I considers two distinct energy allocation mechanisms of net-reproduction and net-assimilation among individual life-history traits, and explores how they affect the stability of a simple community comprising a size-structured consumer species and an unstructured resource species. The two mechanisms differ in assumption concerning the way of distributing absorbed energy between maintenance and reproduction. The net-assimilation mechanism assumes that a fixed fraction of absorbed energy is used for reproduction and the remaining is shared by somatic growth and metabolism. In contrast, the net-reproduction mechanism argues that obtained energy should meet the metabolic demands with a top priority and the surplus, if there is any, is then distributed between somatic growth and reproduction. Further, the distribution in the net-reproduction mechanism in this paper is extended to be size-dependent. By rewriting the size-structured population model to coupled delay-differentiation equations and isolating the characteristic equations the roots of which determine the stability of equilibrium solutions, the extinction boundary and stability boundary are successfully traced as a function of two free parameters. Results show that the net-reproduction mechanism tends to destabilize community dynamics but promotes the coexistence of the two species.

Paper II attempts to integrate two closely related but historically separated subfields of community ecology: size spectrum and food web, two representations of an ecological community. An unstructured population model of Lotka-Voltterra type is developed and species are characterized by two traits: body size and habitat location. The two traits are employed to scale the bioenergetic requirements and represent the spatial distribution of populations, respectively. They act together to determine the type and strength of interactions between individuals of different trait values. Communities are obtained by performing ecological community assembly from predetermined species pools. The two community representations are compared in terms of the exponent of community size spectrum, maximal trophic level, and invasion resistance towards alien species. It is concluded that there is a robust reconciliation between the two representations, in particular for species-rich communities.

Paper III looks at the size-spectrum representation of marine communities, dynamics of which is described by a trait-based size-spectrum model. The essential question addressed here is how the growth variability induced by traits affects the dynamics of marine size spectrum both linearly and nonlinearly. Only one trait (i.e. maximum body size) is used to represent species taxonomic identity. For comparison, a community size-spectrum is derived from the trait-based model, which ignores species identity. The two models produce disparate predictions on the dynamics of marine size spectrum. As apposed to the community size-spectrum model, the trait-based models are more likely to have stable equilibrium solutions. In case of non-equilibrium solutions, trait-based model tends to have much slower, smaller and more regular oscillations than the community size-spectrum model. The reason responsible for this is the growth variability among the individuals of the same body

size but with different trait values, which is initiated by the inclusion of trait.

Paper IV considers the food-web representation of an ecological community with size-structured populations characterized by maturation size. four types of density-dependent interference competition are modeled explicitly at the individual level, namely interference in foraging, metabolism, survival and recruitment. Ecologically, the net outcome between interference induced gain and cost determines qualitatively whether interference is costly or beneficial in affecting population demographic properties. Evolutionarily, although all promoting the speciation in a monomorphic population environment by intensifying the disruptive strength, the four interference mechanisms differ considerably in the evolution of maturation size, either depressing (foraging and metabolism) or elevating (survival and recruitment) the evolutionary equilibrium. Moreover, only survival interference is able to produce highly diverse communities with complex trophic structure through species coevolution and speciation. Finally, there is no clear positive dependence of the final diversification on the initial diversification, and the most diverse communities do not necessarily possess the highest trophic level.

Paper I

Effects of growth curve plasticity on size-structured population dynamics

Zhang L., Lin Z.G., Pedersen M., 2012. Effects of growth curve plasticity on size-structured population models, *Bulletin of Mathematical Biology* 74, 327-345.

Bull Math Biol (2012) 74:327–345
DOI 10.1007/s11538-011-9675-z

ORIGINAL ARTICLE

Effects of Growth Curve Plasticity on Size-Structured Population Dynamics

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Received: 3 March 2011 / Accepted: 16 June 2011 / Published online: 16 July 2011

Abstract The physiological-structured population models assume that a fixed fraction of energy intake is utilized for individual growth and maintenance while the remaining for adult fertility. The assumption results in two concerns: energy loss for juveniles and a reproduction dilemma for adults. The dilemma results from the possibility that adults have to breed even if metabolic costs fail to be covered. We consider a size-structured population model, where standard metabolism is given top priority for utilizing energy intake and the surplus energy, if there is any, is distributed to individual growth and reproduction. Moreover, the portion of surplus energy for reproduction is size-dependent and increases monotonically with size. Using the newly developed parameter continuation, we demonstrate their disparate effects on population dynamics. Results show that the size-dependent mechanism of energy allocation primarily exerts destabilizing effects on the system but considerably promotes species coexistence, in comparison with the size-independent mechanism. We conclude that the size-dependent mechanism is, to a large extent, a dispensable component of model ingredients when ontogeny is explicitly taken into consideration.

Keywords Characteristic equation · Dynamic energy budget theory · Life history · Parameter continuation · Size structure

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1 Introduction

A pronounced scenario in aquatic ecosystems is individual ontogeny. During that course individual body size could range from the egg size of milligram up to several kilogram. The size alteration apparently affects individual life-history including feeding, growth, fertility and mortality, since body size is considered to be the most important parameter governing biological processes (Weitz and Levin 2006). Taking individual ontogenetic growth and life-history into account, structured models are usually used to describe population dynamics (Cushing 1992; de Roos 2008; Andersen and Pedersen 2010).

In general, there are three types of structured population models, that is, age-structured population models (Cushing 1992), physiological-structured population models (de Roos and Persson 2001), and trait-based size-structured population model (Hartvig et al. 2011). The fundamental difference between the first two types of models is that the transition from one stage to the next takes place automatically in the former models (which is out of our interest) but food-dependently in the latter. The trait-based structured model synthesizes the physiological-structured modeling and the community size-spectrum modeling (Andersen and Beyer 2006). It aims to provide a generic framework for size-structured food webs since species are characterized by trait (i.e. size at maturation) avoiding dealing with specific species. However, it can be reparameterised for particular ecosystems.

Built on the framework of physiological-structured population modeling, de Roos et al. (2010) studied the dynamics of Daphnia (de Roos et al. 1990). They developed a numerical program to continuously trace the stability boundaries where Hopf-bifurcations occur as functions of some parameters (e.g. background mortality). In this model, they assumed that a fixed proportion of energy intake is distributed to individual growth and maintenance activities while the remaining to fertility if individuals have matured. Therefore, a questions arises what happens to the remaining energy for juveniles since there is no reproduction involved. In addition, the distributed energy for growth and maintenance might be insufficient to cover metabolic costs. In case of this situation, adults have to breed even during starvation, a reproduction dilemma.

Based on those two concerns, Hartvig et al. (2011) argued that ingested energy should be firstly used for standard metabolism and secondly for growth and reproduction if there is any energy left. Moreover, the distribution of energy between growth and fertility should be dependent on individual size. Apparently, different mechanisms of energy allocation create distinct feedbacks on individual growth curve plasticity via reproduction and food intake. Therefore, our question is how differently the two strategies of energy allocation affect population dynamics.

To examine this question, we reparameterise the trait-based size-structured population model according to the Daphnia model (de Roos et al. 1990) and apply the newly developed numerical tool (de Roos et al. 2010). Specifical model description is presented in the next section. The paper is structured as follows. In Sect. 3, a coupled delay system associated with (6)–(8) is introduced in order to trace the existence and stability boundaries of equilibrium. Section 4 is devoted to derive the characteristic equation to the delayed system. We trace the existence boundary of equilibrium and

stability boundary of positive steady states in Sect. 5. Discussion about the effects of the growth curve plasticity upon the system is carried out in the last section. The work ends up with a brief conclusion.

2 Consumer-Resource Dynamics

The model is composed of a size-structured population Daphnia $N(m)$ (number per unit volume) and an unstructured resource algal R (cells per unit volume). Body size m refers to individual weight (gram).

Food uptake rate of individual m, denoted by $I(m, R)$, depends on the resource density following a Holling type II function response:

$$I(m, R) = \gamma_s m^n f_r(R), \tag{1}$$

where $f_r(R) = \frac{\rho R}{1+\rho R}$, and $\gamma_s m^n$ is the search volume. The maximum amount of energy assimilated per unit time is

$$A(m, R) = \alpha h m^n f_r(R), \tag{2}$$

where α is the assimilation efficiency, and the quotient, h/γ_s, indicates the energy content per algal cell (de Roos et al. 1990). The ingested energy is first used to pay respiration cost, $k_s m$ (West et al. 2001). The remaining surplus energy is then used for individual growth and reproduction, distributed by an allocation function (Hartvig et al. 2011):

$$\psi(m) = \left(\frac{m}{m_\infty}\right)^{0.25} \left(1 + \left(\frac{m_a}{m}\right)^{\xi}\right)^{-1}, \tag{3}$$

where m_∞ is the maximum body size and m_a the maturation size. $\psi(m)$ is a monotonous increasing function of body size with $0 \le \psi(m) \le 1$, and shows that juveniles could reproduce before reaching maturation size m_a (governed by the parameter ξ). The effect of this energy allocation is to generate biphasic growth trajectory, where juveniles grow almost linearly while adults follow the von Bertalanffy growth curves (Lester et al. 2004).

The individual growth rate and reproduction rate can be formulated as (Hartvig et al. 2011):

$$g(m, R) = \max\{A(m, R) - k_s m,\ 0\}\big(1 - \psi(m)\big) \tag{4}$$

and

$$\beta(m, R) = \frac{\varepsilon}{m_0} \max\{A(m, R) - k_s m,\ 0\}\psi(m), \tag{5}$$

where ε is the reproduction efficiency and m_0 is the size at birth (gram). Individuals suffer from the background mortality μ_b only, but die instantaneously when standard metabolism fails to be satisfied.

Table 1 Model symbols and default values

Symbol	Value	Unit	Interpretation
Variable			
K	–	cell·ml^{-1}	Resource carrying capacity
μ_b	–	d(ays)$^{-1}$	Background mortality
Parameter			
λ	9.0×10^{-6}	g·mm^{-3}	Length-mass scaling constant[1]
ρ	7.0×10^{-6}	ml·cell^{-1}	Shape parameter of functional response
γ_s	4.16×10^{9}	cell·g$^{-\frac{2}{3}}$· d^{-1}	Factor of search volume
h	0.6420	g$^{\frac{1}{3}}$·d^{-1}	Factor of maximum consumption rate
n	$\frac{2}{3}$	–	Exponent of maximum feeding rate
α	0.3	–	Assimilation efficiency[2]
ε	0.0081	–	Reproduction efficiency
k_s	0.45	d^{-1}	Factor of standard metabolism
m_0	4.6080	μg	Size at birth
m_a	140.6250	μg	Size at maturation
ξ	10	–	Width of allocation function[3]
r_0	0.5	d^{-1}	Resource growth rate
κ	0.5	–	Allocation efficiency[4]
δ	1.0×10^{-9}	–	Survival threshold[5]

[1]Claessen and de Roos (2003); [2]Andersen and Beyer (2006); [3]Hartvig et al. (2011); [4]Ranging from 0.3 (de Roos et al. 1990) to 0.7 (Claessen and de Roos 2003); [5]de Roos et al. (2010). The remaining are derived from de Roos et al. (1990) based on the mass-length relation $m = \lambda L^3$, where L is body length. Varying parameter values will be specified

Finally, at population level, dynamics of $N(m)$ is described by the McKendric-von Foerster equation:

$$\frac{\partial N(m,t)}{\partial t} = -\frac{\partial (g(m,R)N(m,t))}{\partial m} - \mu(m,R)N(m,t), \quad m \in [m_0,\ m_\infty], \tag{6}$$

subjected to a nonlocal boundary condition reflecting the reproduction flux:

$$g(m_0,R)N(m_0,t) = \int_{m_0}^{m_\infty} \beta(m,R)N(m,t)\,dm. \tag{7}$$

Resource follows the logistic dynamics:

$$\frac{dR(t)}{dt} = f(R) - \int_{m_0}^{m_\infty} I(m,R)N(m)\,dm, \tag{8}$$

where $f(R) = r_0 R(1 - R/K)$. Initial conditions for species N and resource R are ignored since we only focus on the steady states of system (6)–(8). Relevant symbols are summarized in Table 1.

3 Delayed System

Define

$$R_t(\tau) = R(t+\tau), \quad \tau \in (-\infty, 0], \tag{9}$$

which is a resource history at time t. Define $m(a, R_t)$ to be the size that an individual has at age a and time t, given that it has experienced history R_t in the time interval $[t-a, t]$. Likewise, define $F(a, R_t)$ as the survival probability of an individual to reach age a at time t provided that it experiences the resource history in the time interval $[t-a, t]$. Then body size m and survival probability F can be determined as functions of some ordinary differential equations via those vital rates of feeding $I(m, R)$, assimilation $A(m, R)$, growth $g(m, R)$, fertility $\beta(m, R)$, and mortality $\mu(m, R)$. In addition, these rates are smooth mappings from $\Re_+^2$ to $\Re_+$.

In a similar manner to Diekmann et al. (2010), define $\tilde{m}(\zeta) = \tilde{m}(\zeta; a, \Psi)$ as the size of an individual at age ζ, given that it has experienced resource history Ψ in the time interval $[-a, 0]$ at age a, if still alive. Likewise, define $\tilde{F}(\zeta; a, \Psi)$ as the survival probability of an individual that can survive up to age ζ, given that at age a, if still alive, it has experienced resource history Ψ. $\tilde{m}(\zeta; a, R_t)$ and $\tilde{m}(\zeta; a, R_t)$ can be solved through a set of autonomous ordinary differential equations:

$$\begin{cases} \tilde{m}'(\zeta) = g(\tilde{m}(\zeta), \Psi(-a+\zeta)), & 0 \le \zeta \le a, \\ \tilde{m}(0) = m_0 \end{cases} \tag{10}$$

and

$$\begin{cases} \tilde{F}'(\zeta) = -\mu(\tilde{m}(\zeta), \Psi(-a+\zeta))\tilde{F}(\zeta), & 0 \le \zeta \le a, \\ \tilde{F}(0) = 1. \end{cases} \tag{11}$$

Then, we have

$$m(a, R_t) = \tilde{m}(a; a, R_t) \quad \text{and} \quad F(a, R_t) = \tilde{F}(a; a, R_t).$$

Denote by $b(t)$ the population birth rate (number of offspring per volume) per unit time at time t and by $a_\infty (\le \infty)$ the maximum lifetime of an individual under unlimited food conditions. According to Diekmann et al. (2010), the population dynamics of system (6)–(8) can be described by the following system:

$$b(t) = \int_0^{a_\infty} \beta\big(m(a, R_t), R(t)\big) F(a, R_t) b(t-a)\, da, \tag{12}$$

$$R'(t) = f\big(R(t)\big) - \int_0^{a_\infty} I\big(m(a, R_t), R(t)\big) F(a, R_t) b(t-a)\, da. \tag{13}$$

The above system is composed of a renewal equation (12) and a delayed differential equation (13). Initial conditions are ignored since we are restricted to stationary solutions.

Clearly, a trivial equilibrium to system (12) and (13) is $(b^*, R^*) = (0, K)$. Since it is out of our interests, we disregard it here and concentrate on the interior positive

equilibria from now on. A nontrivial equilibrium can be given through the following stationary equations:

$$\Gamma\left(R^*\right) - 1 = 0, \tag{14}$$

$$f\left(R^*\right) - \Theta(R^*)b^* = 0, \tag{15}$$

$$\Gamma\left(R^*\right) := \int_0^{a_\infty} \beta\left(m\left(a, R^*\right), R^*\right) F\left(a, R^*\right) da, \tag{16}$$

$$\Theta\left(R^*\right) := \int_0^{a_\infty} I\left(m\left(a, R^*\right), R^*\right) F\left(a, R^*\right) da. \tag{17}$$

From the biological perspective, $\Gamma(R^*)$ is the expected lifetime offspring reproduction number per adult and $\Theta(R^*)$ is the expected lifetime resource consumption of a consumer individual.

Equation (14) implies that each consumer, at steady state, produces on average one offspring to replace itself during its lifetime. Recall the fertility rate (5), and we see that $\Gamma(0) < 1$ and $\Gamma(\infty) > 1$. In combination with the feeding rate (1), there is a unique solution to equation (14). Once R^* is known, the population birth rate at steady sate is attainable:

$$b^*\left(R^*\right) = \frac{f(R^*)}{\Theta(R^*)}. \tag{18}$$

Therefore, the equilibrium issue to (12) and (13) boils down to find the root of equation (14). In fact, it can be calculated through the following four ordinary differential equations:

$$\begin{aligned} &\frac{d}{da} m\left(a, R^*\right) = g\left(m\left(a, R^*\right), R^*\right), \quad a > 0, \\ &\quad m\left(0, R^*\right) = m_0, \end{aligned} \tag{19}$$

$$\begin{aligned} &\frac{d}{da} F\left(a, R^*\right) = -\mu\left(m\left(a, R^*\right), R^*\right) F\left(a, R^*\right), \quad a > 0, \\ &\quad F\left(0, R^*\right) = 1, \end{aligned} \tag{20}$$

$$\begin{aligned} &\frac{d}{da} \gamma\left(a, R^*\right) = \beta\left(m\left(a, R^*\right), R^*\right) F\left(a, R^*\right), \quad a > 0, \\ &\quad \gamma\left(0, R^*\right) = 0, \end{aligned} \tag{21}$$

$$\begin{aligned} &\frac{d}{da} \theta\left(a, R^*\right) = I\left(m\left(a, R^*\right), R^*\right) F\left(a, R^*\right), \quad a > 0, \\ &\quad \theta\left(0, R^*\right) = 0. \end{aligned} \tag{22}$$

One of our targets is to trace the nontrivial equilibrium as a function of some parameters, denoted by a vector $\overline{\alpha} := (\alpha_1, \ldots, \alpha_l)$. Rewrite system (14)–(15) as

$$\Gamma\left(\overline{\alpha}, R^*\right) - 1 = 0, \tag{23}$$

$$b^* = \frac{f(\overline{\alpha}, R^*)}{\Theta(\overline{\alpha}, R^*)}. \tag{24}$$

The curve induced by

$$f\left(\overline{\alpha}, R^*\right) = 0 \tag{25}$$

and (23) is called the existence boundary for the nontrivial equilibrium (b^* switches sign from negative to positive if this curve is crossed in the appropriate sense in the space defined by (23) and (25)).

We will use (19)–(22) and (23)–(24) to numerically make a track of the existence boundaries of equilibria.

4 Characteristic Equation

To obtain the characteristic equation, whose dominant eigenvalue determines the local stability of equilibrium (b^*, R^*), we linearize (12)–(13) at steady state.

4.1 Linearization of the Coupled Delay System

For convenience, define

$$\begin{aligned} &\beta(a) := \beta\left(m\left(a, R^*\right), R^*\right), \qquad \beta_1(a) := \frac{\partial}{\partial y}\beta(y, R)|_{(y,R)=(m(a,R^*),R^*)}, \\ &F(a) := F\left(a, R^*\right), \qquad \beta_2(a) := \frac{\partial}{\partial R}\beta(x, R)|_{(m,R)=(m(a,R^*),R^*)}. \end{aligned} \tag{26}$$

g_i, I_i and μ_i $(i = 1, 2)$ are defined similarly. These derivatives will be specified in the next section. In addition, assume that $K(a, \lambda)$ and $L(a, \lambda)$ are solutions of the two differential equations:

$$\begin{aligned} &\frac{\partial}{\partial a}K(a, \lambda) = g_1(a)K(a, \lambda) + g_2(a)e^{\lambda a}, \quad a > 0, \\ &K(0, \lambda) = 0, \end{aligned} \tag{27}$$

$$\begin{aligned} &\frac{\partial}{\partial a}L(a, \lambda) = -\mu(a)L(a, \lambda) - \mu_1(a)K(a, \lambda)F(a) - \mu_2(a)F(a)e^{\lambda a}, \quad a > 0, \\ &L(0, \lambda) = 0, \end{aligned} \tag{28}$$

where λ is a complex number.

Differentiating equations (12) and (13) with respect to $b(t)$ and $R(t)$, and evaluating the resulting equations at steady state (b^*, R^*) give rise to the following two equations:

$$v(t) = \int_0^{a_\infty} \beta(a)F(a)v(t-a)\,da + s(t)b^* \int_0^{a_\infty} \beta_2(a)F(a)\,da$$

$$+ b^* \int_0^{a_\infty} F(a)\beta_1(a) D_2 x\big(a, R^*\big) s_t \, da$$
$$+ b^* \int_0^{a_\infty} \beta(a) D_2 F\big(a, R^*\big) s_t \, da, \tag{29}$$

and

$$\frac{ds(t)}{dt} = f'\big(R^*\big)s(t) - \int_0^{a_\infty} I(a)F(a)v(t-a)\,da$$
$$- s(t)b^* \int_0^{a_\infty} I_2(a)F(a)\,da - b^* \int_0^{a_\infty} F(a)I_1(a)D_2 x\big(a, R^*\big)s_t \, da$$
$$- b^* \int_0^{a_\infty} I(a) D_2 F\big(a, R^*\big) s_t \, da, \tag{30}$$

where the two derivatives, $D_2 x(a, R^*)$ and $D_2 F(a, R^*)$, are to be determined.

It assumes that perturbations $u(t)$ and $s(t)$ at the steady state (b^*, R^*) are of the forms $v(t) = e^{\lambda t} b^*$ and $s(t) = e^{\lambda t} R^*$. According to de Roos et al. (2010; Eqs. A.12 and A.13), we then have

$$D_2 m\big(a, R^*\big) s_t = R^* e^{\lambda(t-a)} K(a, \lambda), \tag{31}$$
$$D_2 F\big(a, R^*\big) s_t = R^* e^{\lambda(t-a)} L(a, \lambda). \tag{32}$$

4.2 Derivation of Characteristic Equation

Inserting $u(t) = e^{\lambda t} b^*$ and $s(t) = e^{\lambda t} R^*$ into (29)–(30) and dividing the resulting equations by $e^{\lambda t}$ yield that

$$1 = \int_0^{a_\infty} \beta(a)F(a)e^{-\lambda a}\,da + R^* \int_0^{a_\infty} \beta_2(a)F(a)\,da$$
$$+ R^* \int_0^{a_\infty} F(a)\beta_1(a)e^{-\lambda a}K(a,\lambda)\,da + R^* \int_0^{a_\infty} \beta(a)e^{-\lambda a}L(a,\lambda)\,da, \tag{33}$$

$$\lambda R^* = f'\big(R^*\big)R^* - b^* \int_0^{a_\infty} I(a)F(a)e^{-\lambda a}\,da$$
$$- b^* R^* \int_0^{a_\infty} I_2(a)F(a)\,da - b^* R^* \int_0^{a_\infty} F(a)I_1(a)e^{-\lambda a}K(a,\lambda)\,da$$
$$- b^* R^* \int_0^{a_\infty} I(a)e^{-\lambda a}L(a,\lambda)\,da. \tag{34}$$

Set

$$\Phi_1\big(R^*, \lambda\big) = \int_0^{a_\infty} e^{-\lambda a}\beta(a)F(a)\,da, \tag{35}$$
$$\Phi_2\big(R^*, \lambda\big) = -\int_0^{a_\infty} e^{-\lambda a} I(a)F(a)\,da, \tag{36}$$

$$\Phi_3(R^*,\lambda) = \int_0^{a_\infty} \beta_2(a)F(a)\,da + \int_0^{a_\infty} e^{-\lambda a}\big(\beta(a)L(a,\lambda) + \beta_1(a)F(a)K(a,\lambda)\big)\,da, \tag{37}$$

$$\Phi_4(R^*,\lambda) = -\int_0^{a_\infty} I_2(a)F(a)\,da + \int_0^{a_\infty} e^{-\lambda a}\big(I(a)L(a,\lambda) + I_1(a)F(a)K(a,\lambda)\big)\,da. \tag{38}$$

Then the characteristic equation can be expressed as

$$\det\left(M(b^*,R^*,\lambda) - \begin{pmatrix} 1 & 0 \\ 0 & \lambda \end{pmatrix}\right) = 0, \tag{39}$$

where

$$M(b^*,R^*,\lambda) = \begin{pmatrix} \Phi_1(R^*,\lambda) & \Phi_2(R^*,\lambda) \\ \Phi_3(R^*,\lambda) & f'(R^*) + b^*\Phi(R^*,\lambda) \end{pmatrix}. \tag{40}$$

Recalling (24), we obtain an equivalent form of the characteristic equation as follows:

$$\begin{aligned} 0 = {} & f(R^*)\big((\Phi_1(R^*,\lambda)-1)\Phi_4(R^*,\lambda) - \Phi_2(R^*,\lambda)\Phi_3(R^*,\lambda)\big) \\ & + \Theta(R^*)\big(\Phi_1(R^*,\lambda)-1\big)\big(f'(R^*)-\lambda\big). \end{aligned} \tag{41}$$

For any given steady state, its corresponding eigenvalue spectrum can be computed through (41), and the associated linear stability can be decided. Specifically, if all roots of the characteristic equation have negative real parts, the steady state is locally stable, otherwise, unstable if there is at least one root with positive real part.

4.3 Stability Boundary of Equilibrium

The aim of this subsection is to trace the stability boundaries of equilibria where bifurcations occur. To this end, set $\lambda = i\omega$ ($\omega > 0$) and split the entries in (40) into two real equations:

$$\Phi_j(R^*,\lambda) = \Phi_j^r(R^*,\omega) + i\Phi_j^i(R^*,\omega), \quad j = 1,\ldots,4, \tag{42}$$

where the supindices r and i refer to 'real' and 'imaginary'. Thus, we have

$$\begin{aligned} 0 = {} & H(R^*,\omega) \\ := {} & f(R^*)\left(\big(\Phi_1^r(R^*,\omega)-1\big)\begin{pmatrix}\Phi_4^r(R^*,\omega)\\ \Phi_4^i(R^*,\omega)\end{pmatrix} + \Phi_1^i(R^*,\omega)\begin{pmatrix}-\Phi_4^i(R^*,\omega)\\ \Phi_4^r(R^*,\omega)\end{pmatrix}\right) \\ & + f(R^*)\left(-\Phi_3^r(R^*,\omega)\begin{pmatrix}\Phi_2^r(R^*,\omega)\\ \Phi_2^i(R^*,\omega)\end{pmatrix} + \Phi_3^i(R^*,\omega)\begin{pmatrix}\Phi_2^i(R^*,\omega)\\ -\Phi_2^r(R^*,\omega)\end{pmatrix}\right) \\ & + \Theta(R^*)\left(f'(R^*)\begin{pmatrix}\Phi_1^r(R^*,\omega)-1\\ \Phi_1^i(R^*,\omega)\end{pmatrix} + \omega\begin{pmatrix}\Phi_1^i(R^*,\omega)\\ 1-\Phi_1^r(R^*,\omega)\end{pmatrix}\right). \end{aligned} \tag{43}$$

Incorporating the free parameters $\overline{\alpha}$ into (43), we gain a system of three real equations (H comprises of two equations):

$$\begin{aligned} G\left(\overline{\alpha}, R^*\right) &= 0, \\ H\left(\overline{\alpha}, R^*, \omega\right) &= 0, \end{aligned} \tag{44}$$

where function $G(\overline{\alpha}, R^*) = \Gamma(\overline{\alpha}, R^*) - 1$. Equations (44) define a curve of dimension $l-1$, the stability boundary of equilibrium.

Keep it in mind that the unknown complex functions $K(a, i\omega)$ and $L(a, i\omega)$ are involved in the characteristic equations (41). Analogously to $\Phi_j(R^*, i\omega)$, we rewrite them as

$$K(a, i\omega) = K^r(a) + iK^i(a), \qquad L(a, i\omega) = L^r(a) + iL^i(a), \tag{45}$$

which lead to the following two systems (for $a > 0$):

$$\begin{aligned} \frac{dK^r(a)}{da} &= g_1(a)K^r(a) + g_2(a)\cos(\omega a), \\ \frac{dK^i(a)}{da} &= g_1(a)K^i(a) + g_2(a)\sin(\omega a), \\ K^r(0) &= 0, \quad K^i(0) = 0, \end{aligned} \tag{46}$$

and

$$\begin{aligned} \frac{dL^r(a)}{da} &= -\mu(a)L^r(a) - \mu_1(a)F(a)K^r(a) - \mu_2(a)F(a)\cos(\omega a), \\ \frac{dL^r(a)}{da} &= -\mu(a)L^i(a) - \mu_1(a)F(a)K^i(a) - \mu_2(a)F(a)\sin(\omega a), \\ L^r(0) &= 0, \qquad L^i(0) = 0. \end{aligned} \tag{47}$$

With the real functions $K^r(a)$, $K^i(a)$, $L^r(a)$, and $L^i(a)$ at hand, Φ_j^r and Φ_j^i ($j = 1, \ldots, 4$) can be determined via the following real ordinary differential equations:

$$\begin{aligned} \frac{d}{da}\Phi_1^r(a) &= \beta(a)F(a)\cos(\omega a), \quad a > 0, \\ \frac{d}{da}\Phi_1^i(a) &= -\beta(a)F(a)\sin(\omega a), \quad a > 0, \\ \Phi_1^r(0) &= \Phi_{1,\,0}^r, \quad \Phi_1^i(0) = \Phi_{1,\,0}^i, \end{aligned} \tag{48}$$

$$\begin{aligned} \frac{d}{da}\Phi_2^r(a) &= \beta_2(a)F(a) + \beta(a)L_e^r(a,a) + \beta_1(a)F(a)K_e^r(a,a), \quad a > 0, \\ \frac{d}{da}\Phi_2^i(a) &= \beta(a)L_e^i(a,a) + \beta_1(a)F(a)K_e^i(a,a), \quad a > 0, \\ \Phi_2^r(0) &= \Phi_{2,\,0}^r, \quad \Phi_2^i(0) = \Phi_{2,\,0}^i, \end{aligned} \tag{49}$$

$$\begin{aligned}
&\frac{d}{da}\Phi_3^r(a) = -I(a)F(a)\cos(\omega a), \quad a > 0,\\
&\frac{d}{da}\Phi_3^i(a) = I(a)F(a)\sin(\omega a), \quad a > 0,\\
&\Phi_2^r(0) = \Phi_{3,\,0}^r, \quad \Phi_3^i(0) = \Phi_{1,\,0}^i,
\end{aligned} \tag{50}$$

$$\begin{aligned}
&\frac{d}{da}\Phi_4^r(a) = -I_2(a)F(a) - I(a)L_e^r(a,a) - I_1(a)F(a)K_e^r(a,a), \quad a > 0,\\
&\frac{d}{da}\Phi_4^i(a) = -I(a)L_e^i(a,a) - I_1(a)F(a)K_e^i(a,a), \quad a > 0,\\
&\Phi_4^r(0) = \Phi_{4,\,0}^r, \quad \Phi_4^i(0) = \Phi_{4,\,0}^i,
\end{aligned} \tag{51}$$

where the initial conditions are zero since all the vital rates are continuous in age and resource concentration, and in addition

$$\begin{aligned}
K_e^r(a_1,a_2) &:= K^r(a_2)\cos(\omega a_1) + K^i(a_2)\cos(\omega a_1),\\
K_e^i(a_1,a_2) &:= K^i(a_2)\cos(\omega a_1) - K^r(a_2)\cos(\omega a_1),
\end{aligned} \tag{52}$$

$$\begin{aligned}
L_e^r(a_1,a_2) &:= L^r(a_2)\cos(\omega a_1) + L^i(a_2)\cos(\omega a_1),\\
L_e^i(a_1,a_2) &:= L^i(a_2)\cos(\omega a_1) - L^r(a_2)\cos(\omega a_1).
\end{aligned} \tag{53}$$

To evaluate the entries of the characteristic matrix (40) for given steady state (R^*, b^*), we can integrate (48)–(51), (46)–(47), and (19)–(22) simultaneously. Once the characteristic equations (41) are known, the stability of the steady state is available. Varying the value of parameter $\overline{\alpha}$, the stability boundary of equilibrium can be traced. The population birth rate can be additionally computed via (41). In case of discontinuous vital rates (e.g. reproduction rate which occurs upon maturation), one can refer to de Roos et al. (2010) for detailed treatment.

5 Parameter Continuation

In this section, we shall trace the existence and stability boundaries of equilibria, using the numerical program developed by de Roos et al. (2010) to (23)–(24) and to (44), respectively. However, the numerical scheme is updated by using the Keller's method to perform continuation instead of the method introduced by de Roos et al. (2010). The Keller's parameter continuation is the most natural method for parameter continuation (Kuznetsov 1994).

The existence and stability boundaries of equilibrium are traced as functions of two free parameters, denoted by α_1 and α_2. The resource carrying capacity K and the background mortality μ_b are used in the sequel. All boundaries are projected to the $\alpha_1 - \alpha_2$-plane. The information involved in these figures is discussed in the next section. To decide when those integrations stop, we use the criterion introduced by Kirkilionis et al. (2001) that a_∞ is the age at which the probability of surviving up to

this age has decreased to δ. Since the mortality is constant, therefore,

$$a_\infty = -\frac{\log(\delta)}{\mu_b}. \tag{54}$$

5.1 Reference Model

To see the effects of the growth curve plasticity on population dynamics, we use the following model as a reference. This model is the same as ours except for the distribution of energy, which obeys the rule adopted in de Roos et al. (1990). Specifically, the growth and birth rates are

$$g_c(m, R) = \max\{\kappa A(m, R) - k_s m,\ 0\} \tag{55}$$

and

$$\beta_c(m, R) = \frac{\varepsilon}{m_0}(1-\kappa)A(m, R), \quad m_a \le m \le m_\infty. \tag{56}$$

The calculations of the characteristic equations are ignored throughout this paper and only results are presented.

The maximum body size can be determined through (55) under ideal food condition, which means $f(R) = 1$. As individual approaches the maximum size, individuals stop growing. Thus, at m_∞ we have

$$\kappa\alpha h m_\infty^n = k_s m_\infty,$$

which leads to

$$m_\infty = \left(\frac{\kappa\alpha h}{k_s}\right)^{\frac{1}{1-n}}.$$

Here, the m_∞ is the same as in (3). The differences in growth rate, growth trajectory and fertility rate between the two energy distributions are graphically exhibited in Fig. 1.

5.2 Tracing Existence Boundary of Equilibrium

We choose two free parameters, K and μ_b. The (14) and (18), used to trace the existence boundary of equilibrium, can be rewritten as

$$\Gamma(\alpha_1, R^*) - 1 = 0, \qquad \alpha_2 = R^*. \tag{57}$$

The three-dimensional continuation reduces to be two dimensional. Hence, the boundary in α_1–α_2-plane is equivalent to the curve describing how the equilibrium varies with one parameter. Setting

$$G(\alpha_1, R^*) = \Gamma(\alpha_1, R^*) - 1, \tag{58}$$

then $G(\alpha_1, R^*) = 0$ defines a curve, i.e. the existence boundary of equilibrium. Applying the continuation scheme (de Roos et al. 2010) to the equations $G(\alpha_1, R^*) = 0$ and (19)–(21), the existence boundary is able to be demonstrated (dashed curve in Fig. 2).

Recall that the mortality rate is independent of body size and resource concentration. Equation (21) can be solved explicitly as

$$F(a) = e^{-\mu_b a}, \quad a > 0, \tag{59}$$

which can be used directly during parameter continuation.

5.3 Tracing Stability Boundary of Equilibrium

In contrast with the existence boundary of equilibrium, tracing the stability boundary of equilibrium is mathematically challenging. Recall the equations (44) and the two free parameters, we have

$$\begin{aligned} G\big(\alpha_1, \alpha_2, R^*\big) &= 0, \\ H\big(\alpha_1, \alpha_2, R^*, \omega\big) &= 0. \end{aligned} \tag{60}$$

The above three equations with four variables define a three dimensional surface, i.e. the stability boundary of equilibrium.

To implement the parameter continuation with (60), we have to specify the ingredients in (26) at equilibrium, which are used to evaluate the entries of the characteristic matrix. Concretely,

$$\begin{aligned} g_1(a) &= \big(n\alpha h f_r\big(R^*\big)m^{n-1} - k\big)\big(1 - \psi(m)\big) \\ &\quad - \big(\alpha h f_r\big(R^*\big)m^n - km\big)\frac{d\psi(m)}{dm}, \\ g_2(a) &= \alpha h m^n f_r'\big(R^*\big)\big(1 - \psi(m)\big), \\ \beta_1(a) &= \frac{\varepsilon}{m_0}\big(n\alpha h f_r\big(R^*\big)m^{n-1} - k\big)\psi(m) \\ &\quad + \frac{\varepsilon}{m_0}\big(\alpha h f_r\big(R^*\big)m^n - km\big)\frac{d\psi(m)}{dm}, \\ \beta_2(a) &= \frac{\varepsilon}{m_0}\alpha h m^n f_r'\big(R^*\big)\psi(m), \\ I_1(a) &= n\gamma_s m^{n-1} f_r\big(R^*\big), \qquad I_2(a) = \gamma_s m^n f_r'\big(R^*\big), \\ \mu_1(a) &= 0, \qquad \mu_2(a) = 0, \end{aligned} \tag{61}$$

where

$$\begin{aligned} f_r'\big(R^*\big) &= \frac{\rho}{(1 + \rho R^*)^2}, \\ \frac{d\psi(m)}{dm} &= \psi(m)\left(\frac{0.25}{m} + \frac{\xi m^{-1}}{1 + (\frac{m}{m_a})^{\xi}}\right). \end{aligned} \tag{62}$$

Since $\mu_1(a) = \mu_2(a) = 0$, it is easy to see from (47) that both $L^r(a)$ and $L^i(a)$ are zero. Moreover, $L_e^r(a_1, a_2)$ and $L_e^i(a_1, a_2)$ in (53) are zero as well. Then the ordinary differential equations in (49) and (51) reduce to

$$\begin{aligned}
&\frac{d}{da}\Phi_2^r(a) = \beta_2(a)F(a) + \beta_1(a)F(a)K_e^r(a,a), \quad a > 0,\\
&\frac{d}{da}\Phi_2^i(a) = \beta_1(a)F(a)K_e^i(a,a) + \beta_1(a)F(a)K_e^r(a,a), \quad a > 0, \qquad (63)\\
&\Phi_2^r(0) = 0, \quad \Phi_2^i(0) = 0,\\
&\frac{d}{da}\Phi_4^r(a) = -I_2(a)F(a) - I_1(a)F(a)K_e^r(a,a), \quad a > 0,\\
&\frac{d}{da}\Phi_4^i(a) = -I_1(a)F(a)K_e^i(a,a), \quad a > 0, \qquad (64)\\
&\Phi_4^r(0) = 0, \quad \Phi_4^i(0) = 0.
\end{aligned}$$

It is now ready to carry out the parameter continuation on the stability boundary of positive equilibrium with equations (60). To evaluate (60), one has to integrate (48), (50), (63), and (64) together with (46) and (19)–(22) simultaneously. The resulting stability boundary is demonstrated and projected to the two-dimensional parameter space, i.e. $\alpha_1 - \alpha_2-$ plane (solid curve in Fig. 2).

In addition, the two distinguished stability boundaries of equilibria, corresponding to different types of energy distribution are demonstrated in Fig. 3. For convenience, the traditional distribution of energy is referred to as size-independent allocation while the other as the size-dependent allocation. As examples, some combinations of parameters are chosen to show the population dynamics via equations (6)–(8) (Fig. 4). Finally, stability boundaries for different proportions of ingest energy that is allocated to growth and maintenance, are illustrated in Fig. 5.

6 Discussion and Conclusion

The model in de Roos et al. (1990) assumes that κ percent of the total ingested energy is allocated for individual growth and maintenance. The allocation implies a loss of energy for juveniles (Fig. 1a), compared to the case of size-dependent allocation (Fig. 1c). The consequence is that juvenile growth rate is slowed down, prolonging the immature period subsequently. On the other hand, the remaining energy ($1 - \kappa$ percent) is used for adult reproduction indicating that much energy for reproduction is consumed for individuals upon maturing (Fig. 1b).

6.1 Existence and Stability Boundaries

The existence and stability boundaries are exhibited in Fig. 2. The equation (23) suggests that an interior equilibrium exists if $\Gamma(\mu_b, K) > 1$. Below the existence boundary, i.e. Region I, there is only a trivial equilibrium $(K, 0)$. Taking the background mortality μ_b and resource carrying capacity K as the bifurcation parameters,

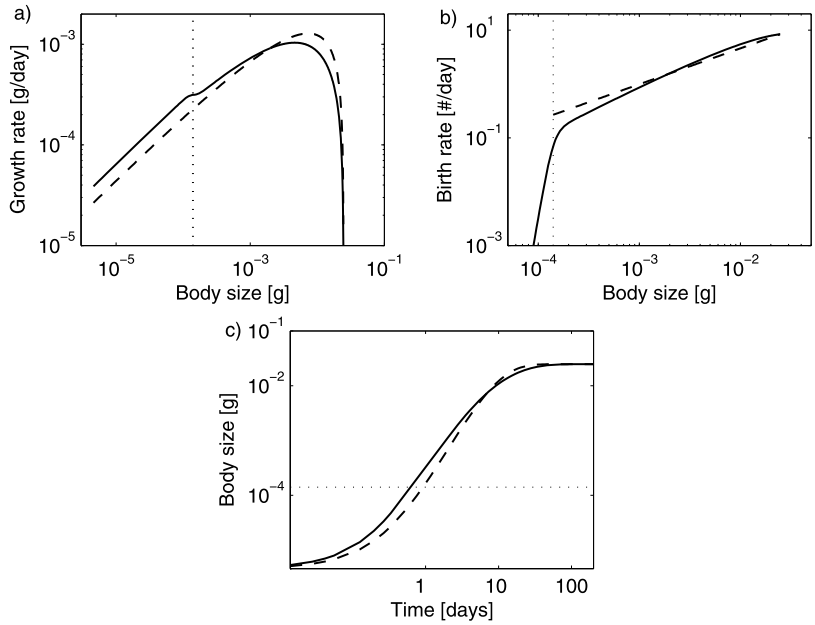

Fig. 1 Individual growth rate (**a**), birth rate (**b**) and growth trajectory (**c**) under ideal food condition and default parameter values in Table 1 except for $\kappa = 0.7$. *Solid* and *dashed curves* respectively indicate the size-dependent and -independent allocation of ingested energy. *Dotted lines* denote the maturation size

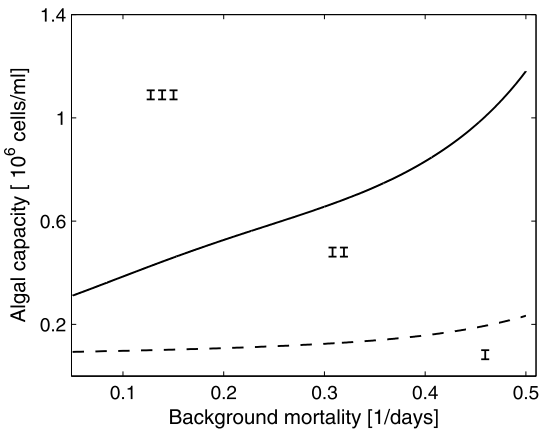

Fig. 2 Existence (*dashed*) and stability (*solid*) boundaries of equilibria for the size-dependent allocation of ingested energy under default parameter values in Table 1. Region I indicates that interior positive equilibrium does not exist, Region II the stable equilibrium and Region III the unstable equilibrium

the branch of interior equilibrium bifurcates from the trivial steady state. The general results from bifurcation theory implies that the interior equilibrium is stable when the carrying capacity is slightly greater than the steady state (de Roos et al. 1990). Hence, the equilibria are stable in Region II but unstable in Region III. Two particular examples, i.e. $(\mu_b, K) = (0.4, 4 \times 10^5)$ and $(\mu_b, K) = (0.4, 9 \times 10^5)$, are made to demonstrate the population dynamics through integrating equations (6)–(8). The exhibition in Fig. 4 (left panels) is exactly as predicted by the stability diagram.

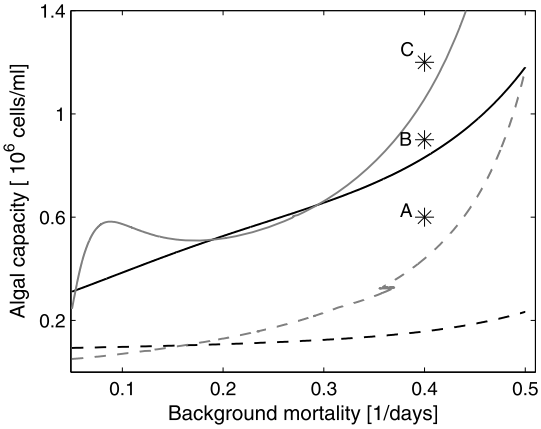

Fig. 3 Existence (*dashed*) and stability (*solid*) boundaries of equilibria corresponding to the size-dependent (*black*) and independent (*grey*) allocations of energy under default parameter values in Table 1. Stars $A = (0.4, 6 \times 10^5)$, $B = (0.4, 9 \times 10^5)$ and $C = (0.4, 1.2 \times 10^6)$ are chosen as examples to illustrate the dynamics of Daphnia and algal at population level (Fig. 4)

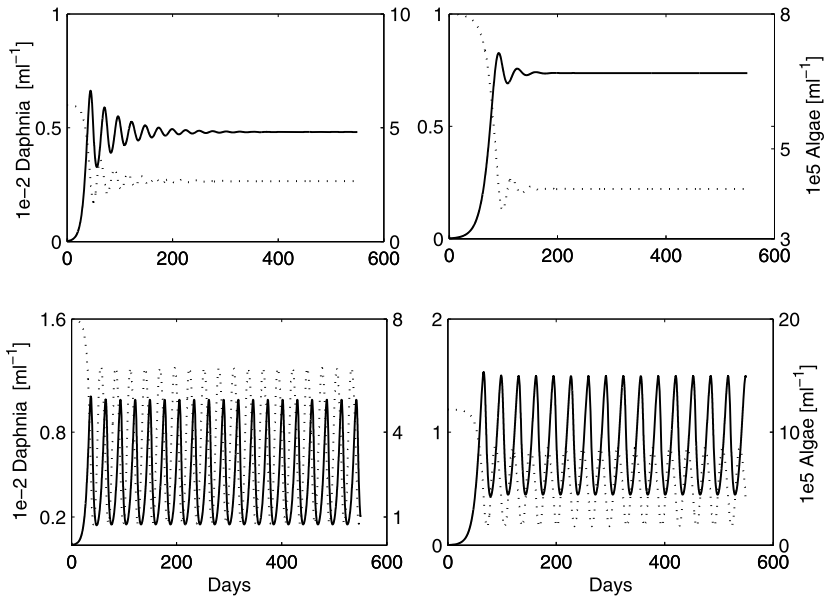

Fig. 4 Time-dependent Daphnia population biomass (*solid*) and algal concentration (*dotted*) under default parameter values in Table 1. The *left panels* correspond to the stars A and B in Fig. 3 for size-dependent allocation of energy, while the *right* ones the stars B and C in Fig. 3 for size-independent allocation of energy. Initial conditions are $N(0, m) = m^{-2.05} \times 10^{-9}$ for Daphnia and $R(0) = K$ for algal

Figure 2 reveals three features: (1) Increasing background mortality stabilizes population dynamics for given algal carrying capacity. It arises from that large mortality suppresses the growth of Daphnia population and in turn relieves the predation pressure on algal. This is identified to be the mechanism of life-history of Daphnia (de Roos et al. 1990). (2) Increasing resource carrying capacity destabilizes population dynamics for given background mortality. The reason behind it is as follows. Food availability of Daphnia individuals increases with increased resource carrying capacity, which leads to rapid growth in size, shortening the immature period and raising

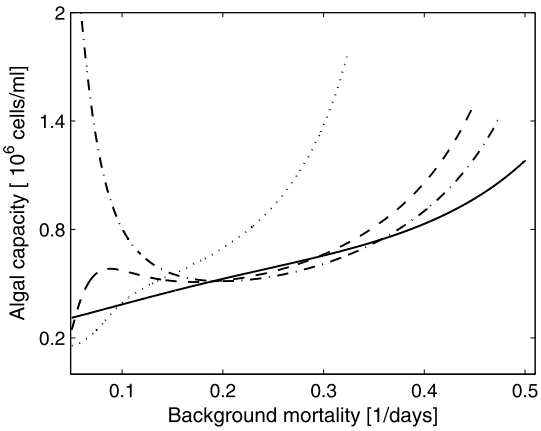

Fig. 5 Comparison diagram of stability boundaries for the size-dependent allocation of energy (*solid*) and the size-independent allocation of energy under default parameter values in Table 1 except for $\kappa = 0.3$ (*dotted*), $\kappa = 0.5$ (*dashed*), and $\kappa = 0.6$ (*dot-dashed*)

adults density consequently. As population abundance rises, algal density declines dramatically. The decrease of algal population leads to the drop of fertility, growth and the total population of Daphnia. This induces the onset of the next cycle (Fig. 4). It is identified as the prey escape mechanism (de Roos et al. 1990). (3) The stable region increases with increasing mortality and resource capacity. It results from the interplay between the prey escape mechanism and the control of the life-history of Daphnia.

6.2 Comparison of Energy Distribution Mechanisms

In comparison with the size-independent energy allocation, it is easy to see the following patterns from Fig. 3. Generally, for large background mortality, the size-dependent allocation destabilizes the system but considerably favors the coexistence of Daphnia and algal (e.g. Fig. 4). Nevertheless, for certain combinations of resource capacity and mortality, the size-dependent allocation stabilizes population dynamics, typically for small K and μ_b.

Regarding the stability boundary, Fig. 5 demonstrates additional three patterns: (1) the size-dependent allocation of energy produces the largest unstable region while the size-independent allocation for $\kappa = 0.3$ gives rise to the smallest unstable region. (2) Stable regions shrinks with increasing κ for large values of μ_b and K but broadens for small values. (3) For the intermediate values of μ_b and K, the overlapping area between size-dependent and independent allocation increases with increased κ.

The life-history of Daphnia accounts for these observations. On one hand, increasing the allocation efficiency in size-independent allocation of energy leads to rapid individual growth. Two effects take place consequently. One is the shorter immature period and the other the larger mean size. The shorten juvenile stage results in the aggregation of adults, which subsequently enhances the possibility of producing more offspring. The increase in mean size suggests a higher feeding rate. Nonetheless, the energy for individual birth rate declines as κ increases. In spit of the declined birth rate, the first effect exerts a destabilizing influence on system through the prey escape mechanism. On the contrary, the second one imposes a stabilizing influence since the mean size is in exact antiphase with the oscillation of Daphnia density, reducing

consequently the impact of these oscillations on the algal population (de Roos et al. 1990). On the other hand, taking individual birth rate and mortality rate into consideration, the stabilizing effect is the determining factor of affecting system stability for small mortality rate but gradually replaced by the destabilizing effect as mortality increases. However, the destabilizing influence is primary in the case of size-dependent allocation of energy regardless of the background mortality rate. It is because the maturation delay is substantially reduced since all energy after paying respiration cost is fully utilized by juvenile growth.

So far, we have demonstrated the disparate effects of the two energy allocation mechanisms on the dynamics of Daphnia and algal. It remains unclear which mechanism operates among organisms. One the one hand, the standard dynamic energy budget (DEB) theory demonstrates that standard metabolism has priority of utilizing energy intake over all other activities (Sousa et al. 2010), even though there exists evidence showing that some organisms are still able to reproduce (e.g. Kirk 1997), or to grow (e.g. Gallardo et al. 2004), when energy intake is insufficient to cover metabolic costs.

On the other hand, the standard DEB theory assumes no competition between growth and reproduction, that is, a constant proportion of net energy (total energy minus maintenance cost) is partitioned to production. In this regard, the size-independent mechanism of energy allocation essentially follows the DEB theory. A consequence of the fixed proportion is the von Bertalanffy growth for both juveniles and adults. However, as advocated by Lester et al. (2004), juveniles grow almost linearly while adults grow in the mode of the von Bertalanffy growth curve, yielding a biphasic growth trajectory. The growth mode implies that the proportion of net energy assigned to growth decreases monotonically with size (Kooijman 2000; Nisbet et al. 2004), with which the size-dependent mechanism of energy allocation is in consistence. Moreover, from the empirical perspective, Nisbet et al. (2010) tested that size-dependent proportion of energy channeled to growth is a key requirement in order to obtain good match of model with data on Daphnia population dynamics, indicating the significance of size-dependent mechanism of energy allocation.

In summary, we explored the impacts on population dynamics of the growth curve plasticity determined respectively by the size-dependent and -independent mechanisms of energy allocation. Existence and stability boundaries were continuously traced using the recently developed numerical scheme. Results revealed the disparate effects between the two energy allocation strategies. The former strategy tend to destabilize population dynamics but promote species coexistence, in comparison with the other strategy. Taking individual ontogenetic growth and life history into consideration, we conclude that the size-dependent mechanism of energy allocation is, to a large extent, an important component of model ingredients.

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Paper II

The relationship between food-web and size-spectrum representations of communities

Zhang L., Hartvig M., Knudsen K., Andersen K.H., 2011. The relationship between food-web and size-spectrum representations of communities (*Manuscript*).

The relationship between food-web and size-spectrum representations of communities

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Abstract

A food web describes a community as a finite number of interacting species. In contrast, a size spectrum disregards species identity and only describes the abundance distribution against individual body size. Here we study to which degree the predictions of the two approaches are in correspondence. To this end, we develop a trait-based model of Lotka-Volterra type, where each species is characterized by two traits: body size and habitat location, from which trophic and competitive interactions emerge. The model is solved using four approaches: analytical approximations as a size spectrum and as a trophic chain, and numerical food-web assembly from discrete and continuous species pools. We focus on three aspects: community size-spectrum exponent, constraints on the maximum trophic level (MTL), and community stability in terms of invasion resistance. It is found that the size-spectrum exponents estimated from the four approaches are almost identical. While the trophic-chain approach shows the energetic constraints on MTL, the food-web approach reveals that the MTL is jointly determined by energetic constraints, structural constraints, and ecosystem size. Invasion resistance only captured food-web model and communities are equally vulnerable to intruders regardless of the size of the species pool. In conclusion, we find good correspondence between food-web and size-spectrum representations but the degree to which the size-spectrum presentation is approximated depends on the species richness of food webs.

Keywords: community assembly, food web, size-spectrum exponent,

1. Introduction

Trait-based models are emerging as a means of describing communities as interacting individuals characterized by one or more traits (Norberg et al., 2001; Bruggeman et al., 2007; Merico et al., 2009). The result of a trait-based model is the abundance of individuals as a function of their trait values. The central assumption of trait-based models is that it is more insightful to consider individuals in terms of their traits instead of which species they belong to. This stands in stark contrast to almost all other community modelling approaches for which the species concept is central.

In trait-based models the traits can be seen as a parametrization of a species. Since traits can be either continuous or discrete, it is in principle possible to work with infinitely or finitely many species in the same framework, as a consequence of which is the continuous or discrete community representation. As both representations are abstract forms of the same underlying community, their results should be compatible, however, no systematic comparison of continuous and discrete approaches has been carried out.

A trophic community can be represented by considering individuals as belonging to a trophic level without considering their species (Lindeman, 1942). A modern variant of this representation is the community size-spectrum (Sheldon et al., 1972) describing the density distribution of individuals as a function of body size (i.e. body mass) irrespective of their species identity. In a log-log plot, the relationship between density and body size is predicted to be a straight line having a slope of around -2 (Kerr, 1974; Silvert and Platt, 1980; Benoît and Rochet, 2004; Andersen and Beyer, 2006). We consider the size-spectrum as an example of a continuous description of a trophic community.

A trophic community may also be represented as a food web, where individuals are organized in a discrete number of species. Species are represented by nodes which are connected via links that indicate the feeding relationship between taxonomically different species. Food-web representation therefore illustrates the trophic positions of interacting species and has long been the subject of extensive study in community ecology (e.g. May, 1972; Brose et al., 2006; Rossberg et al., 2008; Kondoh and Ninomiya, 2009). In the food

web each species may be characterized by one or more traits as in the size-spectrum representation. The central difference however is that the trait represented in the community is considered as a discrete set rather than as the continuous distribution in the size-spectrum representation. In this work, a food web is used as an example of a discrete description of a trophic community.

The aim of this work is to question to which degree the continuous (size-spectrum) and discrete (food-web) representations of the same model system lead to compatible results. We analyze the correspondence between the continuous and discrete representations of a community, or, more concretely, the degree to which the communities calculated from assembled food webs correspond to the continuous size-spectra. To this end, we develop a classical Lotka-Volterra based model where all rates are allometrically scaled with body size (Yodzis and Innes, 1992). The interaction matrix is defined by a novel size- and trait-based approach that combines a habitat trait with predator-prey interactions determined by body size. This property enables a direct comparison between the discrete and the continuous representations by considering the limit of the number of species going towards infinity where the trait space is fully filled.

The model is analyzed using four different approaches, each involving different assumptions. Each solution represents a point on the continuum between a fully continuous solution and fully discrete solution: (i) a size-spectrum solution based on an assumption of continuous distribution of an infinite number of species, leading to a prediction of size-spectrum exponent; (ii) a trophic-chain solution where species are pooled into discrete trophic levels, leading to predictions of community exponent and the highest trophic level that can persist in the community; and fully numerical community assembly of food web using (iii) discrete and (iv) continuous species pools (Morton and Law, 1997; Law, 1999). The first two approaches consider only the trait of body size. They are based on the flow of energy within the community, and define energetic limits to abundance and maximum trophic level. The last two approaches consider both trait dimensions. The third solution represents a true discrete representation of a community whereas the fourth representation, based on a continuous species pool, may be considered intermediate between the size spectrum and the food web. The four solutions are compared by focusing on three community-level measures: the exponent of community size spectrum, the maximum trophic level, and the community stability in terms of resistance to alien invasions.

2. Model description

The model is based on individual-level processes. Species are characterized by a size trait m and a habitat trait x (size is given in terms of mass and habitat is dimensionless). A body size trait is employed to scale individual physiological rates (e.g. the rates of search volume and respiration) while the habitat trait may be thought of as a population's spatial location and distribution; for simplicity a one-dimensional abstract representation of space is used (Hartvig, 2011). The spatial distribution of species i's population is assumed to be Gaussian-shaped with a center at x_i, and the width of the distribution is increasing monotonically with body size m_i. Interactions between spatially co-occurring organisms take place through predation following the rule of "big-eat-small".

Population dynamics N_i (number of individuals per unit volume) within the community is inspired by the consumer-resource model by Yodzis and Innes (1992)

$$\begin{aligned}\frac{dN_i}{dt}\frac{1}{N_i} = & \underbrace{\varepsilon\gamma m_i^q m_i^{-1}\int m_0 N_0(x)\varphi(m_i/m_0)\psi(x_i-x)dx}_{\text{Gain from resource}} \\ & \underbrace{+\varepsilon\gamma m_i^q m_i^{-1}\sum_j m_j N_j\varphi(m_i/m_j)\psi(x_i-x_j)}_{\text{Gain from consumer species}} \\ & -\underbrace{\tilde{k}m_i^{n-1}}_{\text{Metabolism}} \underbrace{-\sum_j \gamma m_j^q N_j\varphi(m_j/m_i)\psi(x_j-x_i)}_{\text{Loss due to predation}},\end{aligned} \tag{1}$$

where individuals within consumer species N_i obtain food from resources $N_0(x)$ (hereafter denoted by N_0) and other smaller consumer species with a mass-dependent volumetric search rate γm_i^q. After paying the cost of metabolism $\tilde{k}m_i^{n-1}$, the remaining energy is translated into population growth with a conversion efficiency ε. Population abundance is regulated by predation from larger species.

Individual interactions are described by a size-selection kernel $\varphi(m_i/m_j)$ and a spatial interaction kernel $\psi(x_i - x_j)$. They determine when predation occurs and their product constitutes the interaction strength. The size-selection function is a lognormal function (Ursin, 1973), describing the pref-

erence of m_i sized individuals to m_j sized individuals

$$\varphi(m_i/m_j) = \exp\left(-\left(\log^2 \frac{m_i}{\beta m_j}\right)/(2\sigma_m^2)\right) \tag{2}$$

that peaks when m_i/m_j equals the preferred predator-prey mass ratio β. Thus, individuals with mass ratio far from β have negligible interactions. The range of prey sizes a predator can consume is determined by the width of the selection function σ_m.

The spatial kernel $\psi(x_i - x_j)$ assumes the abundance of individuals within a species N_i to be normally distributed in space with a center at x_i, and returns the strength of the interaction which is given by the spatial overlap of the interacting populations (Hartvig, 2011)

$$\psi(x_i - x_j) = \frac{1}{\sqrt{2\pi(\sigma_x^2(m_i) + \sigma_x^2(m_j))}} \exp\left(\frac{-(x_i - x_j)^2}{2(\sigma_x^2(m_i) + \sigma_x^2(m_j))}\right). \tag{3}$$

Here, the width of species spatial distribution $\sigma_x(m_i)$ is the home range, which is an increasing function of body size (Kramer and Chapman, 1999; Haskell et al., 2002; Jetz et al., 2004)

$$\sigma_x(m_i) = \sigma_0 + \frac{1}{2}\log_{10}(m_i/m_0), \tag{4}$$

where σ_0 is the home range of m_0 sized species.

Resource abundance N_0 is described using logistic growth and assumed to be continuously distributed along the spatial direction x with constant carrying capacity K

$$\frac{dN_0}{dt}\frac{1}{N_0} = \underbrace{\tilde{r} m_0^{n-1}\left(1 - \frac{N_0}{K}\right)}_{\text{Intrinsic growth rate}} - \underbrace{\sum_j \gamma m_j^q N_j \varphi(m_j/m_0)\psi(x_j - x)}_{\text{Loss due to predation}}, \tag{5}$$

where the intrinsic growth rate is scaled with body size as $\tilde{r} m_0^{n-1}$ (Savage et al., 2004). m_0 is resource body size and also the smallest size of consumer species. Resource abundance is controlled by predation from consumer species.

To avoid the dependence of our results on the specific choices of m_0 and γ, equations (1) and (5) are scaled by setting $\tau = t\gamma m_0^q$, $w_j = m_j/m_0$. The

Table 1: Model parameters

Parameter	Value	Interpretation
β	100	Preferred predator-prey mass ratio
ε	0.2	Conversion efficiency
q	0.75	Exponent of volumetric search rate[¶]
n	0.75	Exponent of metabolic costs
k	3.3	Prefactor for metabolic costs
σ_m	1	Width of selection function
σ_0	$\sqrt{2}/2$	Home range of m_0 sized species
Δx	50	Ecosystem size
r	30	Prefactor for the scaled resource generation rate[§]
K	510#/vol	Resource carrying capacity[§]

[¶]Theoretically expected value is 0.8 (Andersen and Beyer, 2006). $q = n$ is to ease analytical analysis.
[§]Adjusted to produce up to 6 trophic levels with resource sitting at the first trophic level. The remaining are from Hartvig (2011).

equations for biomass $B_j = w_j N_j$ are then

$$\frac{dB_0}{d\tau}\frac{1}{B_0} = r\left(1-\frac{B_0}{K}\right) - \sum_j w_j^{q-1} B_j \varphi(w_j)\psi(x_j - x), \tag{6}$$

$$\frac{dB_i}{d\tau}\frac{1}{B_i} = \varepsilon w_i^{q-1}\left(\int B_0\varphi(w_i)\psi(x_i - x)dx + \sum_j B_j\varphi(w_i/w_j)\psi(x_i - x_j)\right) - kw_i^{n-1} - \sum_j w_j^{q-1} B_j\varphi(w_j/w_i)\psi(x_j - x_i), \tag{7}$$

where $r = \tilde{r}m_0^{n-q-1}/\gamma$ and $k = \tilde{k}m_0^{n-q-1}/\gamma$. As a result, γ and m_0 disappear from the system, leading to two new parameters r and k. Parameter values are given in Table 1.

The total spatial size of the ecosystem is set to be $\Delta x = 50$ ($\gg \sigma_x(w_{max})$) such that the largest species ($w_{max} \sim 10^{10}$) have sufficient room for roaming. We use periodic boundary condition in the spatial direction.

3. Results

In this section, the model (6)−(7) is analyzed analytically as a size spectrum (Section 3.1) and as a trophic chain (Section 3.2), and numerically as community assembly from discrete and continuous species pools (Section 3.3).

In Section 3.1 and 3.2 below we ignore the habitat trait to facilitate analytic solutions.

3.1. Size-spectrum solution

Assume a continuum of species along the body size direction, that is, the body size varies continuously from w_0 to w_{max}. Then equation (7) can be rewritten as

$$\begin{aligned}\frac{dN}{Nd\tau} &= \varepsilon w^{q-1}\int_{w_0}^{w_{max}} N(w')\varphi(w/w')dw' \\ &\quad -\int_{w_0}^{w_{max}} w'^{(q-1)}N(w')\varphi(w'/w)dw' - kw^{n-1}. \end{aligned} \tag{8}$$

The equilibrium of the above equation (i.e. $dN/d\tau = 0$) is assumed to be a power-law state, i.e. $N(w) = \rho_0 w^{2-\lambda}$, where λ is the size-spectrum exponent (Sheldon et al., 1972), and ρ_0 is a constant, reflecting the primary productivity of ecosystems (Cyr et al., 1997). Insert this ansatz into the right-hand side of equation (8) and do the Gaussian integration. To be able to evaluate the integral analytically, the boundary of the integral is relaxed from 0 to ∞. Then, we obtain

$$\varepsilon\beta^{\lambda-2}e^{(\lambda-2)^2\sigma_m^2/2} - \beta^{1+q-\lambda}e^{(1+q-\lambda)^2\sigma_m^2/2} = \frac{k}{\sqrt{2\pi}\rho_0\sigma_m}w^{\lambda-(2+q-n)}. \tag{9}$$

As w enters into the last term in equation (9), (8) does not admit a pure power-law solution in general. If we ignore standard metabolism by setting $k = 0$, we may obtain an approximative solution to λ as follows

$$\lambda \simeq \lambda_1 = \frac{1}{2}\left(3 + q - \frac{\log\varepsilon}{\log\beta + \sigma_m^2(q-1)/2}\right), \tag{10}$$

which is $\lambda_1 = 2.0546$ for the chosen parameter values in Table 1 (for robustness of the approximation, see Table 2 in Section 3.3).

3.2. Trophic-chain solution

The trophic-chain solution is a stationary solution to equation (7) where species are pooled into discrete trophic levels. Mathematically, it is equivalent to a set of species with a separation in weight equal to predator-prey mass

ratio, i.e. $w_i/w_{i-1} = \beta$, and the size selection function $\varphi(s) = 0$ for $s \neq \beta$. Thus, equations (6) and (7) can be written as

$$\begin{aligned} \frac{dB_0}{d\tau}\frac{1}{B_0} &= r(1 - B_0/K) - w_1^{q-1}B_1, \\ \frac{dB_i}{d\tau}\frac{1}{B_i} &= \varepsilon w_i^{q-1}B_{i-1} - kw_i^{n-1} - w_{i+1}^{q-1}B_{i+1},\ i = 1, \cdots. \end{aligned} \tag{11}$$

Taking into account $q = n$ and $w_0 = 1$, we have a linear recurrence relation for equilibrium soltuions

$$\frac{B_{i+1}}{B_{i-1}} = \frac{\varepsilon}{\beta^{q-1}} - \frac{k}{\beta^{q-1}B_{i-1}}. \tag{12}$$

Using the ansatz $B_i \propto w_i^{2-\lambda}$, if we as in Section 3.1 neglect the standard metabolism and put $k = 0$, we can find an approximative exponent explicitly

$$\lambda \simeq \lambda_2 = \frac{1}{2}\left(3 + q - \frac{\log \varepsilon}{\log \beta}\right). \tag{13}$$

(for robustness of the approximation, see Table 2 in Section 3.3). With the chosen parameter values (Table 1) we have $\lambda_2 = 2.0497$.

To sustain a certain number of species (S), it is derived that K and r should at least satisfy

$$Kr > \begin{cases} ra(1 - b^j)/(1 - b) + aK\beta^{q-1}(1 - b^j)/(1 - b), & S = 2j + 1, \\ ra(1 - b^j)/(1 - b) + aK\beta^{q-1}(1 - b^{j-1})/(1 - b), & S = 2j, \end{cases} \tag{14}$$

where $a = k/\varepsilon$, $b = \beta^{q-1}/\varepsilon$ and j is a positive integer. Therefore, increasing K and r prolongs the trophic chain. The given parameter values (Table 1) yield 5 consumer species that coexist along the trophic chain.

3.3. Community assembly

Apart from above analytical approaches, numerical analysis of model (6)−(7) is performed using the approach of sequential community assembly in this subsection. This approach demonstrates a gradual development of a community by introducing species in a low density one by one from a species pool which is a set of species prescribed prior to assembly (Morton and Law, 1997; Law, 1999). On the basis of the emergent communities, the three-level measures (i.e. size-spectrum exponent, maximum trophic level, and community stability) can be computed.

Two types of species pools are employed: discrete and continuous. The discrete pool is comprised of a finite number of species with trait values randomly selected from a 2-dimensional trait space $(x, w) \in \Omega = [-25, 25] \times [1, 10^{11}]$. Four sizes of finite species pools are constructed with 25, 50, 100, and 200 species. For each pool size, 50 pool replicates are generated, and from each species pool 20 communities are assembled yielding 4000 communities in total, 1000 for each pool size. As to the continuous species pool, trait values (x, w) are drawn at random from Ω. In both discrete and continuous cases, x is chosen uniformly while w log-uniformly. The details of the assembly algorithm are given in Appendix A.

The representation of species interactions through traits w and x makes it possible to visualize the process of food-web assembly (Fig. 1). In the pristine environment, the basal resource creates a positive fitness landscape where species with a size of $w \sim \beta$ are able to colonize (Fig. 1A). After the first successful invasion, the fitness landscape is reshaped and a new area of positive fitness values is opened up for predators (Fig. 1B). This process proceeds (Fig. 1C) until none of species in the species pool are able to invade the community, leading to an un-invadable end-state (Fig. 1D). The fitness landscape shows that there are still possibilities for species not part of the species pool (alien species) to invade as there are islands with positive invasion fitness. The decreasing number of species along the mass axis is due to the combined effects of constraints on the structure of the food web and the energetic constraints describing the energy flow from low to high trophic levels.

The tropic structure and the distribution of abundance against body size of the model community are presented in Fig. 2A and 2B. The trophic pattern shows that up to five trophic levels were developed in the end-state. In comparison with species body size, it is easy to see that species trophic position can be approximated by $\log_{10}(w)/2$. Thus, body size turns out to be a good predictor of species trophic position, provided with a given trophic position of resource species. The size-spectrum reveals that the distribution pattern is well approximated by a power law with a spectrum exponent $\lambda = 2.0654$ (corresponding to the slope value -1.0655). The size-spectrum exponent is slightly larger than the predicted values from the size-spectrum solution and trophic-chain solution, where standard metabolism is ignored.

Species from the species pool that possess positive invasion fitness are always present, which is also often true for the discrete species pools of size 200. Consequently, community structure experiences continuous changes as

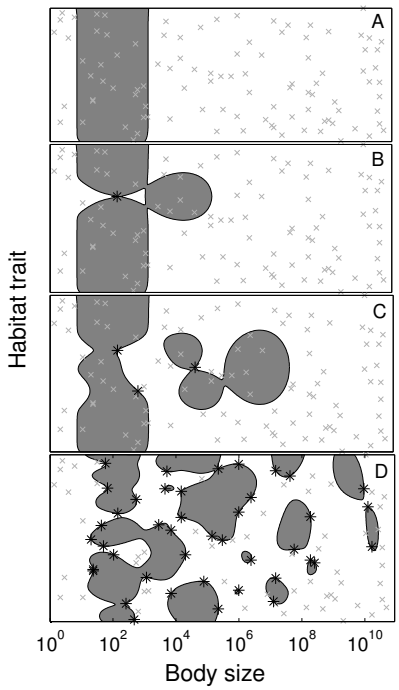

Fig. 1: Assembly of a model community from a finite pool of 100 species (light grey crosses). (A) Fitness landscapes of the pristine environment showing areas where the invasion fitness is positive (grey), (B) after the first successful invasion, (C) after the third successful invasion, and (D) in the final un-invadable end-state (as no species in the species pool have trait values in the grey areas). Positive invasion fitness are exhibited by the grey areas outside which invasion fitness is negative. Successful invaders (stars) sit on the boundaries of the grey islands where fitness is zero. In the final assembled community 41 species coexist. Habitat trait ranges from -25 to 25 in each panel with total ecosystem size equal to $\Delta x = 50$.

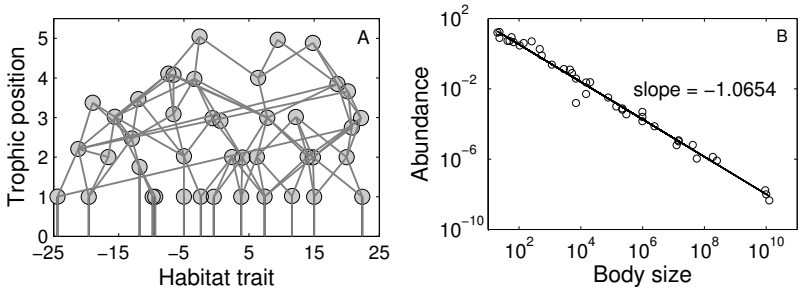

Fig. 2: Trophic structure (A) and size distribution (B) of the assembled community in Fig. 1D. Trophic level is fractional and calculated as the average trophic level of the prey of the focal species plus 1 (Brännström et al., 2011). Resource (continuously distributed) is assumed to be at the lowest trophic position 0. Two species (nodes) are connected from prey (low) to predator (high) if the prey makes a contribution greater than 5% to the diet of predator. The size distribution (solid line) is drawn using a linear regression to species log abundance and log body size. The linear regression yields a slope value of -1.0654, equivalently $\lambda = 2.0654$.

seen from the fluctuation of species richness on the time scale of successful invasion (Fig. 3). The fluctuation is incurred by intermittent extinction avalanches and has plausibly arrived at a regular pattern after an initial short transition (approximately 3000 successful invasions).

Ignore the habitat trait, that is, reducing the 2-dimensional trait space to 1-dimensional, and we demonstrated (Appendix B) that there is a unique evolutionary steady state (ESS), which is an un-invadable end-state (Fig. 4). Apparently, the five coexisting species are roughly spaced by β in the w-trait space. The selections of these positions are mainly because species with mass traits of these values have a selection advantage over the species with intermediate body size. The emergence of this pattern may also be glimpsed from the pool with 100 species (Fig. 1D). The regularity of this pattern may not be found by assembly for 2-dimensional trait space due to the continuous changes in community composition (see Fig. 3), but can however be developed by assembly if only w-trait is considered.

The mean values of the size-spectrum exponent and associated standard deviations across species pools are shown in Fig. 5. In this 'Sheldon' representation of the size distribution (Sheldon et al., 1972), the spectrum exponent

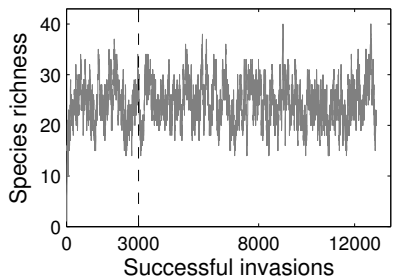

Fig. 3: Species richness of model communities assembled from the continuous species pool as a function of successful invasions. Communities are collected after 3000 successful invasions (dashed line) for calculating community-level measures.

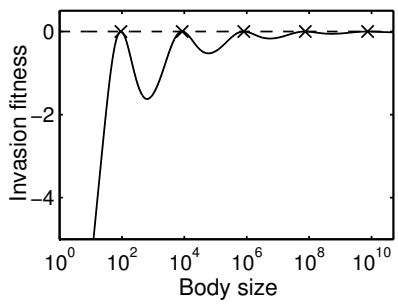

Fig. 4: Fitness landscape of the evolutionary steady state (ESS) to the reduced continuous species pool approach where only mass trait is considered. The ESS is unique and contains five species (crosses) sitting separately on the peaks of the fitness curve with a body size separation that roughly equals predator-prey mass ratio β.

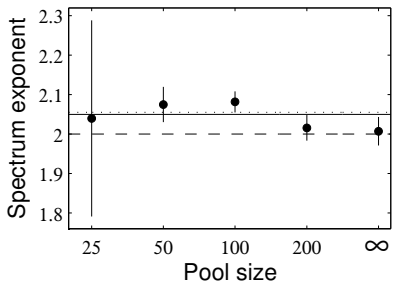

Fig. 5: Mean values (black dots) and standard deviations (vertical lines) of the size-spectrum exponent as a function of the species pool size. The exponents predicted from 'Sheldon' solution (dashed), size-spectrum solution (dotted), and trophic chain solution (solid) are also presented. The result from the continuous species pool is denoted by ∞.

λ exhibits small variations as a function of species pool size. For a specific species pool size, there is a small variation of λ except for the small species pools (25 in our case). The reason for this is that only small webs can be assembled from small species pools due to the sparse species distribution in the mass-habitat trait space. The estimated λ is in general greater than 2, indicating that the average biomass density decreases with increasing trophic level but gets closer and closer to the approximated λ in Section 3.1 and 3.2, as the size of species pool increases.

The maximum tropic level (MTL) that an assembled community can possess varies remarkably within small species pools (e.g. 25, 50) but insignificantly within large species pools as illustrated in Fig. 6. Communities with low trophic levels dominate when assembled from small species pools. With an increase in the species pool size, communities with high trophic levels tend to be dominant. Moreover, the distribution of MTL tends to be stable when species pool size exceeds 100.

The invasion resistance to alien species that belong to the trait space but not the species pool displays a quite small variation across species pool size, when it is measured by the ratio of the areas with negative fitness to the total areas of Ω (Fig. 7).

The size-spectrum and trophic-chain solutions show that the size-spectrum

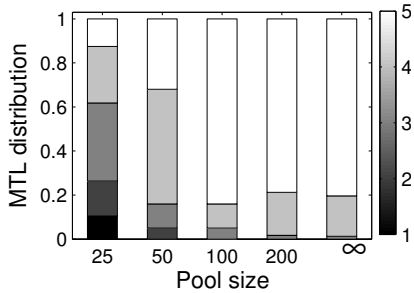

Fig. 6: Proportion of communities with a maximum trophic level (MTL) of 1 (black) to 5 (white) as a function of pool size. The continuous species pool is indicated by ∞.

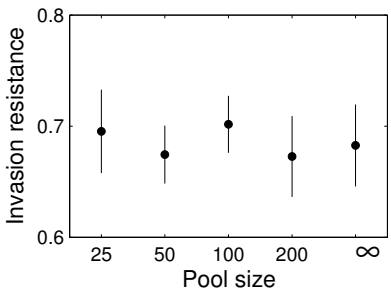

Fig. 7: Mean values (black dots) and standard deviations (vertical lines) of invasion resistance as a function of the species pool size. Invasion resistance is measured as the ratio of the areas with negative fitness (white areas in Fig. 1) to the total area of the trait space Ω.

Table 2: Size-spectrum exponents for varied parameters (bold)

$q^{\dagger}$	$\beta^{\S}$	$\varepsilon^{\P}$	λ_0 (mean ± sd)	λ_1	λ_2
0.75	100	0.2	2.0070 (± 0.0362)	2.0546	2.0497
0.65	100	0.2	1.9504 (± 0.0330)	2.0066	1.9997
0.9	100	0.2	2.0295 (± 0.0850)	2.1267	2.1247
0.75	**20**	0.2	2.0569 (± 0.0555)	2.1553	2.1436
0.75	**500**	0.2	1.9340 (± 0.0402)	2.0071	2.0045
0.75	100	**0.1**	2.0894 (± 0.0277)	2.1320	2.1250
0.75	100	**0.4**	1.9067 (± 0.0798)	1.9787	1.9745
0.8	100	**0.1**	2.0909 (± 0.0318)	2.1555	2.1500
0.8	100	0.2	2.0201 (± 0.0489)	2.0786	2.0747
0.8	**20**	**0.1**	2.2368 (± 0.0639)	2.2976	2.2843
0.8	**500**	**0.1**	2.0232 (± 0.0235)	2.0883	2.0853

†Expected range is [0.62, 1] and widely accepted value is 0.8 (Andersen and Beyer, 2006). §Expected range is [10, 1000] (Andersen et al., 2009). ¶Widely used value is 0.1 (Lewis and Law, 2007) and (Rossberg et al., 2008). $\varepsilon = 0.4$ is biologically unrealistic but it can however provide with valuable insight about the dependence of λ on ε. λ_0 is estimated from the communities assembled from the continuous species pool.

exponent λ varies with some parameters including the preferred predator-prey mass ratio β, the exponent of volumetric search rate q, and the conversion efficiency ε. To see the dependency of λ on these parameters, we estimate λ from the communities assembled from the continuous species pool, and summarize results into Table 2. The reason for employing the continuous species pool is to minimize the impacts on λ of species distribution in Ω, which takes effect when discrete species pools are adopted.

Large volumetric search exponent, small preferred predator-prey mass ratio, and small conversion efficiency raise the size-spectrum exponent and vice versa. Although the effects can be amplified or diminished, depending on the specific parameter combinations, the variations are not significant within the given parameter ranges. The predictions from our size-spectrum and trophic-chain solutions overestimate size-spectrum exponent a little bit, because we ignored the standard metabolism. In particular, for two biologically interesting parameter sets, i.e. $q = 0.8, \beta = 100, \varepsilon = 0.1(0.2)$, spectrum exponents are fairly close to the 'Sheldon' solution, that is, $\lambda = 2$, although exception exists, for example, $q = 0.8, \beta = 20, \varepsilon = 0.1$.

4. Discussion

We examined three aspects of the relationship between the size-spectrum (continuous) and food-web (discrete) representations of communities using a trait-based formulation of a classic Lotka-Volterra model. The difference between the approaches was illustrated by solving the model as a size-spectrum model, as a trophic-chain model, and as a food-web model with discrete and continuous species pools.

Size-spectrum exponent

The representation of a community as a size-spectrum was introduced by Sheldon and Parsons (1967). A general conjecture was that the biomass in logarithmically spaced size groups was constant, or a weakly decreasing function of size (Sheldon et al., 1972), which corresponds to an exponent of the density size-spectrum 2. This conjecture has since then been upheld (Peters, 1983; Boudreau and Dickie, 1992; Schmid et al., 2000) and demonstrated in community size-spectrum models (Benoît and Rochet, 2004; Andersen and Beyer, 2006; Datta et al., 2010; Hartvig et al., 2011).

Our analytical calculations from the size-spectrum and trophic-chain solutions yield $\lambda \simeq 2$, falling within the range of observed size spectra. The analytical solution of the size-spectrum exponent corresponds to the solutions given by Sheldon et al. (1972) for a value of the search volume exponent $q = 1$. If $q \neq 1$ there is a small correction, which is $1/16$ for $q = 3/4$, i.e. quite small. The solution by Sheldon et al. (1972) was based on an assumption about population growth rate scaling as $m^{-3/4}$, but the solution in this model employs a different scaling. Here the population growth rate is not constrained by this metabolic assumption, but is determined by food availability. The constraint of $q = n$ is to ease our analytical computation and quite often not necessary. As seen from Table 2 where this constraint is released, only a slight difference is produced.

In addition, the fact that individuals are not allowed to grow between trophic levels makes the size-spectrum approach implemented in this paper differs from the general size-spectrum models. The latter ones are based on individual growth in body size and mathematical formulated by partial differential equations (Benoît and Rochet, 2004; Andersen and Beyer, 2006; Datta et al., 2010; Hartvig et al., 2011). These models predict the size-spectrum exponent to be $\lambda = 5/4 + q$ (Andersen and Beyer, 2006) or $\lambda \simeq$

$(3+q-\log\varepsilon/\log\beta)/2$ (Datta et al., 2010), which are close to our predictions of λ_1 and λ_2 as well.

When standard metabolism is taken into account in the size-spectrum and trophic-chain solutions, there are no scaling solutions any longer. In both solutions, the spectrum is limited by a maximum size (or equivalent a maximum trophic level), which introduces a correction to the scaling solutions. However, the correction is very slight for trophic levels smaller than the upper trophic levels. Numerical estimation of λ from assembled communities (Table 2) reveals that in both size-spectrum and trophic-chain solutions, the scaling solution may still be considered a good approximation in particular for large food webs. In conclusion, even though there are differences between the predictions from different employed approaches, all predictions are so similar that it will not be possible to distinguish their validity based on comparison with empirical data.

Maximum trophic level

Our analyzes of the maximum trophic level cast light on the debate on which constraint (energetic, structural or habitat size) that determines the length of a food chain. (1) The trophic-chain solution demonstrates that increasing resource availability increases food-chain length. This finding is in agreement with the general energy limitation hypothesis (Lindeman, 1942) where the energetic constraints determined by the resource availability and individual losses (through efficiency and metabolic costs) determine the length of the food chain (Oksanen et al., 1981; Yodzis, 1984; Post, 2002). (2) The structural constraints are determined by the structure of species pool in the mass-habitat trait space: the smaller the pool size, the more heterogeneous the pool structure, and the harder it may be to build a long food chain within the energetic limits. How the heterogeneity affects the food-chain length depends on the specific pool structure. In general, communities with dilute species pools tend to produce food webs with low trophic level (less than 3, Fig. 6). Nevertheless, it is still possible to obtain long food chains given appropriate distribution of species in the pool. As pool size increases, the distribution of species in trait space becomes more homogeneous and the effects of structural constrains are gradually lost. Eventually species tend to be arranged in a trophic chain along the mass-axis with a spacing given by the preferred predator-prey mass ratio β. This observation is in accordance with the prediction by Weitz and Levin (2006). (3) Larger ecosystem size Δx prolongs food chains (Post et al., 2000; Kondoh and Ninomiya, 2009).

As home range is positively correlated with species body size (Kramer and Chapman, 1999; Haskell et al., 2002; Jetz et al., 2004), larger communities can thus naturally accommodate more species. This also agrees with the fact that small ecosystems rarely have large species (Post et al., 2000).

Taken together, the model illustrates that maximum trophic level is not determined solely by energetic constraints, structural constraints or habitat size, but rather all three constraints act in concert, with one of them often taking a dominant role. In this manner the maximum trophic level in a particular system will appear to be limited by just one constraint.

Community stability

The stability of the species assemblage may be characterized in both ecological and evolutionary time scale. On the ecological time scale, stability is considered with regard to stability towards invasions of new species. The communities assembled from the small discrete species pool are stable towards invasions of species from the species pool, but they are always open with regard to alien species, i.e. species not coming from the species pool, due to the existence of islands of positive invasion fitness in trait space.

Even though the assembled communities are stable on the ecological time scale, they are not evolutionarily stable, as evolution on the traits will occur in the direction of the islands with positive invasion fitness. For large species pools (pool size larger than 200 in our case) the communities are generally unstable on both ecological and evolutionary time scales as both alien species and species from the pool can invade. However, reducing the dimension of trait space can lead assembled community to an ESS that is stable on the time scale of both ecology and evolution. This finding infers that increasing the dimension of trait space might alter the nature of the attractor contained in low dimensional trait space. Further, while our community assembly failed to converge to an ESS, it is an open question whether evolutionary simulations, e.g. using adaptive dynamics (Dieckmann and Law, 1996; Dieckmann and Doebeli, 1999) would be able to reach an ESS.

Invasion resistance varies insignificantly with the size of species pool (Fig. 7). This observation suggests that we cannot expect communities assembled from large species pools to be more resistant with respect to alien invasion than from small species pools. For the continuous species pool that represents the total trait space, there are no alien species. Thus, the invasion resistance measures the vulnerability of communities to invaders that are from the species pool. However, the continuous species pool can be envisaged

as the limit of increasing discrete pool size. We conclude that communities of different diversity suffer from a vulnerability to invaders at the same level.

Model architecture

The model is a standard Lotka-Volterra type of population model with size-based allometric scaling of vital rates (Yodzis and Innes, 1992). The interaction matrix of the food-web model has been constructed using a novel, purely trait-based description, with the two traits being body size and habitat location. The use of body size to determine species interaction has become standard in many food-web models (Williams and Martinez, 2004; Brose et al., 2006), but it is always used in conjunction with an interaction matrix with prescribed topological structure. The trait-based description combines the size-based prey selection model with the classic niche-based model for species competition (MacArthur and Levins, 1967) and may be viewed as a generalization of the model used for examining the relation between predation and competition by Chesson and Kuang (2008).

The advantage of the trait-based description of species interactions allows examination of the influence of a discrete (finite species pools) or saturated (continuous species pool) trait space. The combination of body size and habitat size traits makes it relevant to consider that the home range increasingly depends on body size, since larger individuals may roam over a larger area than smaller individuals. If the home range (i.e. σ_x) did not increase with body size, the assembled communities would be more like parallel coupled food chains. The increase of σ_x couples the food web across the habitat trait. This feature is similar to the manner that larger species combine different basal energy pathways in an ecosystem (Rooney et al., 2006). So, even though we have made the x-trait inspired by the spatial extent of a habitat, it is good representation of more abstract notions of food selection choice.

Summary

We have shown that the discrete and continuous representations (food-web and size-spectrum) give predictions of patterns which are not exactly identical, but, except for systems with very low species diversity, indistinguishable in practice, assuming that predictions do not depend on the model framework being employed.

Acknowledgement

Ken Haste Andersen was financially supported by the European FP7 program MEECE.

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Appendices

A. Assembly algorithm

The assembly algorithm is a replicate of Hartvig (2011), but presented below for completeness.

Model communities are formed using sequential assembly by introducing one new species at a time in low density (10^{-10} g/vol) (Post and Pimm, 1983;

Drake, 1990; Law, 1999) from a species pool. If invasion fitness is positive then the system is stimulated till it reaches steady state which can be a fixed point, periodic or even chaotic, detected using heuristic algorithm. Fitness is measured using the per capita population growth rate (i.e. the evaluation of the right-hand side of equation (7)). A species is assumed to be in steady state if its absolute fitness is smaller than $1/1000$ yr^{-1}. During simulation species are removed if they are going to extinction, defined as 1) population biomass falls below the extinction threshold 10^{-20} g/vol, 2) fitness is smaller than $-1/250$ yr^{-1} while the biomass is below 10^{-5} g/vol, or 3) fitness is smaller than $-1/1000$ yr^{-1} while the biomass is below 10^{-10} g/vol. The assembly proceeds to a new invader if the introduced invader has negative invasion fitness, or if the augmented community (resident community plus invader) has reached equilibrium state.

In general, within 300 successful invasion attempts, assembly from species pools with size less than 200 are able to reach an equilibrium state where no species in the pools can invade. However, there is a rare possibility that assembly do not converge, in case of which assembly are terminated after 300 successful invasions. By contrast, assembling communities from a species pool size of 200 very often reaches an oscillating state, where regular pattern in general is obtained after 800 successful invasions. Thus, community is gathered when either assembly has reached an equilibrium state or 800 successful invasions have been attempted (whichever happens first). For continuous species pool, 3000 communities are collected after 3000 successful invasions, after which assembly generally have reached regular patterns. In addition, the continuous species pool is discretized evenly in the x direction with a step size $\delta x = 0.2$ and logarithmically evenly in the w direction with a step size $\delta \log w = 0.1$. Results appear independent on the choice of discretization.

B. Deriving the ESS to the continuous species pool

An ESS means that there reside a certain number of species at steady state and any species with trait values differing from those of the resident species cannot invade. In this section, we consider the one-dimensional continuous species pool, where only body size is included.

To seek for an ESS, we assume that there are p species coexisting with

stationary equations being written as

$$\begin{cases} 0 &= r(1-B_0/K) - \sum_{j=1}^{p} w_j^{q-1} B_j \varphi(w_j), \\ 0 &= \varepsilon w_i^{q-1} \sum_{j=0}^{p} B_j \varphi(w_i/w_j) - k w_i^{n-1} - \sum_{j=1}^{p} w_j^{q-1} B_j \varphi(w_j/w_i), \\ & \quad i = 1, \cdots, p, \end{cases} \tag{B.1}$$

where $w_i > w_{i-1}$. The three necessary conditions under which the p resident species are sitting at ESS are

$$B_i > 0,\ g(w_i) = 0,\ g'(y)|_{y=w_i} = 0, \tag{B.2}$$

where $i = 1, \cdots, p$, and

$$g(w) := \varepsilon w^{q-1} \sum_{j=0}^{p} B_j \varphi(w/w_j) - k w^{n-1} - \sum_{j=1}^{p} w_j^{q-1} B_j \varphi(w_j/w). \tag{B.3}$$

The first two conditions mean that the p species can coexist at the steady state while the last implies that the p species are sitting at the local minimum or maximum on the fitness curve defined by $g(w)$.

Solving (B.2) is mathematically challenging. Noticing that the simulated communities have maximum trophic level of 5 (Fig. 6) and that mass ratios of predator to prey in assembled communities are roughly constant around β (Fig. 1D), it might as well set $p = 5$ and assume that only neighboring resident species interact. With such two constraints, solving (B.2) with Maple gives rise to a solution $(w_1^*, \cdots, w_5^*) = (0.9167 \times 10^2, 0.7953 \times 10^4, 0.7424 \times 10^6, 0.6463 \times 10^8, 0.6463 \times 10^{10})$, which indeed is an ESS as $g(w) \leq 0$ for all w (Fig. 4). Furthermore, numerical examinations demonstrate that there is no other ESS, implying that the evolutionary steady state $(w_1^*, \cdots, w_5^*)$ is unique.

Paper III

Trait diversity promotes stability of community dynamics

Zhang L., Thygesen U.H., Knudsen K., Andersen K.H., 2012. Trait diversity promotes stability of community dynamics, *Theoretical Ecology* doi: 10.1007/s12080-012-01610-6.

Theor Ecol
DOI 10.1007/s12080-012-0160-6

ORIGINAL PAPER

Trait diversity promotes stability of community dynamics

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Received: 12 July 2011 / Accepted: 9 February 2012

Abstract The theoretical exploration of how diversity influences stability has traditionally been approached by species-centric methods. Here we offer an alternative approach to the diversity–stability problem by examining the stability and dynamics of size and trait distributions of individuals. The analysis is performed by comparing the properties of two size spectrum models. The first model considers all individuals as belonging to the same "average" species, i.e., without a description of diversity. The second model introduces diversity by further considering individuals by a trait, here asymptotic body size. The dynamic properties of the models are described by a stability analysis of equilibrium solutions and by the non-equilibrium dynamics. We find that the introduction of trait diversity expands the set of parameters for which the equilibrium is stable and, if the community is unstable, makes the oscillations smaller, slower, and more regular. The stabilizing mechanism is the variation in growth rate between individuals with the same body size but different trait values.

Keywords Life history · Size spectra · Structured population · Trait-based modeling

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Introduction

A central quest in community ecology is to unravel what determines the stability of a community. This question has traditionally been approached from a description of the community as a food web based on unstructured population models (e.g., May 1972; McCann et al. 1998; Kondoh 2003; Dunne et al. 2005; Brose et al. 2006; Gross et al. 2009). As food-web models assign a fixed trophic position to all individuals within a species, they are well suited to describe species where individuals stay within their trophic niche throughout life. An important departure from this pattern is marine communities that are dominated by individuals that grow and change prey throughout life (ontogenetic trophic niche shift). To tackle this type of community, the size-spectrum approach has emerged as a recent alternative to the traditional food-web approach to community dynamics (Silvert and Platt 1978). The size-spectrum models do not incorporate the description of species but rather everything is rooted in the concept of the individual that is only characterized by its body size (i.e., body mass) (Sheldon and Parsons 1967). Since body size is the most important determinant governing the majority of individual ecological processes (Peters 1983; Cohen et al. 1993), the use of size spectrum to characterize the marine communities appears to be an appealing method to reduce a complex community to a simple representation.

The characterization of a marine community as a size spectrum describes a frequency distribution of individual density as a function of body size (Sheldon et al. 1972). Empirical studies have found that a log–log plot of density versus size is roughly a straight line with slope of approximately minus two (Sheldon et al.

Published online: 09 March 2012

1977; Boudreau and Dickie 1992; Kerr and Dickie 2001; Jennings and Mackinson 2003). The biological interpretation is that small organisms in marine ecosystems are more abundant than large ones, but their biomass in logarithmically spaced size groups is approximately invariant. One ecologically important application is that the marine size spectrum could potentially be an indicator of the impacts of human activities on marine ecosystems, in particular on the well-being of the fish communities (e.g., Rice and Gislason 1996; Shin et al. 2005).

A dynamical model of the size spectrum can be constructed by considering the flow of biomass from smaller to larger sizes as a consequence of growth fueled by big organisms eating smaller organisms (Benoît and Rochet 2004; Law et al. 2009). This model is the simplest model that can be formulated of a community dominated by food-dependent growth and has the same role as a minimal model for marine communities that the trophic chain model has for terrestrial communities (e.g., Oksanen et al. 1981). This community size-spectrum model (henceforth referred to as the community model) has been the topic of recent interest both regarding the equilibrium solution (Benoît and Rochet 2004; Datta et al. 2010), the response of the community to fishing (Blanchard et al. 2009; Rochet and Benoît 2011), and the stability of the community (Capitán and Delius 2010; Datta et al. 2011; Plank and Law 2011).

Stability analysis of the community model reveals that the power-law equilibrium of the idealized infinite size spectrum is unstable, regardless of the specific value of parameters (Datta et al. 2011). Some second-order effects can be stabilizing: a growth process based on discrete and random encounters, as opposed to deterministic continuous growth, stabilizes the power-law equilibrium of the size spectrum if the predator–prey mass ratio is small (Datta et al. 2011). Also, if only a short range of body sizes are included in the model, then the equilibrium may be stable (Plank and Law 2011). Finally, analytical calculation indicates that a variation of growth rates between individuals with the same size may have a weak stabilizing effect (Capitán and Delius 2010).

The community model is a crude description of real ecological communities as it does not take any difference between individuals into account, except their size; in particular, there is no representation of species. Note that body size is not a trait, as when size is used to create unstructured food-web models (Yodzis and Innes 1992), but an individual state which changes as the individual grows larger. To accommodate some aspects of species identity and diversity, the trait-based size-spectrum model (referred to as the trait-based model) has been introduced (Andersen and Beyer 2006; Andersen and Pedersen 2010; Hartvig et al. 2011). This model characterizes the individuals both by their instantaneous body size (the state) and by their asymptotic body size (the trait), i.e., the maximum attainable size of the individual. This model therefore represents the community as a two-dimensional distribution of body size and trait.

The differences between the community and the trait-based models beg the question to which degree these two models lead to the same conclusions. If they produce similar conclusions, it means that the additional trait diversity does not make qualitatively changes to the community model and one can probably only focus on the community model due to its simplicity and analytical tractability. On the contrary, if the opposite is true, then the community model may be oversimplified. As a consequence, predictions from the community model might be unreliable. Our first aim focuses on the stability of equilibria in the two models, in particular to which degree the introduction of trait diversity into the community model stabilizes the equilibrium.

The second aim of our work is to describe the dynamical properties of the unstable equilibria of the two models. In general, there is no a priori reason to assume that natural food webs should possess stable equilibria and not display self-induced oscillations (Yodzis 1981). The stability analysis of equilibrium solutions therefore only gives partial insight into community dynamics. By comparing the two models, we demonstrate that the introduction of trait diversity makes the oscillations around the unstable equilibrium solution much smaller.

In summary, the overall purpose of this paper is to clarify how trait diversity stabilizes the equilibrium solutions and affects the dynamics of non-equilibrium solutions of size-spectrum models. To this end, we take care to setup the two models to be as similar as possible by deriving the community model as a special case of the trait-based model. Our analysis consists of four parts: deriving the community model as a special case of the trait-based model, determining the equilibrium solution of both models, examining the stability of the equilibrium solution and its dependence on the parameters related to prey size preference, and describing the dynamics of non-equilibrium solutions for a given individual size, including amplitude, frequency, and the relationship between time average of the non-equilibrium solution and equilibrium state. To concentrate on the ecologically relevant findings, we leave the technical details to "Appendices 1, 2, and 3."

Methods

This section contains three subsections demonstrating, respectively, the description of the trait-based model, the derivation of the community model as an approximation of the trait-based model, and model implementation. The trait-based model is introduced on the basis of Andersen and Beyer (2006), who considered the idealized infinite equilibrium size spectrum. From this description, the averaged growth efficiency for the individuals of the same size but of different trait values is derived (Andersen et al. 2009). The averaged growth efficiency is adopted in the community model. Finally, in the last subsection, we nondimensionalize the parameters and briefly present the ideas of computing equilibrium solutions and determining their stability, as well as how to compute the dynamics of non-equilibrium solutions.

Trait-based model

The trait-based size-spectrum model is governed by the McKendrick–von Foerster equation (McKendrick 1926; von Foerster 1959)

$$\frac{\partial}{\partial t}N(m,M,t) = -\frac{\partial}{\partial m}(g(m,M,t)N(m,M,t)) - \mu(m,t)N(m,M,t). \quad (1)$$

The size spectrum $N(m, M, t)$ (numbers per weight per asymptotic weight per volume) describes individual density distribution as functions of the asymptotic body size M (the trait) and individual body size m (all sizes are given in terms of weight) at time t such that the number of individuals in the size range $[m, m + \mathrm{d}m]$ and trait range $[M, M + \mathrm{d}M]$ is $N(m, M, t)\mathrm{d}m\mathrm{d}M$. m ranges from m_b to M, where m_b is the size of offspring which is the same for all species. Model equations and parameters are summarized in Table 1 and 2.

Predation is the driving force of population dynamics and takes place between individuals with different body sizes obeying the rule of "big-eat-small". Selection of prey of a given individual size is described by a log-normal function (E1) that peaks when the size ratio of predator to prey equals the preferred predator–prey mass ratio β (Ursin 1973). The size range of prey is governed by the diet width σ, and the selection function is normalized into area one such that the smaller the σ, the sharper the peak of the selection function. The encountered food through predation ($E(m, t)$; E2) is multiplied by the growth efficiency ($\varepsilon_I(m, M)$; E3a) to give individual somatic growth rate ($g(m, M, t) = \varepsilon_I(m, M)E(m, t)$; E4a). The growth efficiency, which is a monotonically decreasing function of size, determines the amount of energy routed to individual somatic growth. Growth ceases when individual approaches M. Individuals die due to predation from larger individuals and other natural causes (summarized as the background mortality μ_b) (E5). To account for the recruitment of offspring, we impose a fixed lower boundary condition ($N(m_\mathrm{b}, M)$; E6a), which is trait-dependent ("Appendix 1"). Food for larvae and small individuals is specified by a constant resource spectrum $N_r(m) = \kappa m^{-\lambda}$, $m \le m_\mathrm{b}$.

Derivation of the community model

The community size spectrum is defined as

$$N_\mathrm{c}(m,t) \equiv \int N(m,M,t)\,\mathrm{d}M. \quad (2)$$

Table 1 Model equations

Equation	Interpretation	Number
$\varphi(x) = \exp(-\log^2(x/\beta)/(2\sigma^2))/\sqrt{2\pi\sigma^2}$	Size selection function	E1
$E(m) = \gamma m^q \int w(N_\mathrm{c}(w) + N_r(w))\varphi(m/w)\mathrm{d}w$	Encountered food	E2
$\varepsilon_I(m, M) = \alpha(1 - (m/M)^{r-n})$	Individual growth efficiency	E3a
$\bar{\varepsilon}_I = a\alpha\exp((2n(q-1) - q^2 + 1)\sigma^2/2)/(2 + q - 2n)$	Average growth efficiency	E3b
$g(m, M) = \varepsilon_I(m, M)E(m)$	Growth rate in trait-based model	E4a
$g_\mathrm{c}(m) = \bar{\varepsilon}_I E(m)$	Growth rate in community model	E4b
$\mu(m) = \int \gamma w^q N_\mathrm{c}(w)\varphi(w/m)\mathrm{d}w + \mu_\mathrm{b}$	Mortality rate	E5
$N(m_\mathrm{b}, M) = f_0 M^{2n-q-3+a} m_\mathrm{b}^{-n-a}$	Boundary condition for trait-based model	E6a
$N_\mathrm{c}(m_\mathrm{b}) = \kappa m_\mathrm{b}^{-\lambda}$	Boundary condition for community model	E6b
$N_\mathrm{c}(m) = \int N(m, M)\mathrm{d}M$	Community size spectrum	E7
$N_r(m) = \kappa m^{-\lambda}$	Resource spectrum	E8

The constant f_0 and the physiological predation rate $a = \beta^{2n-q-1}/\alpha$ are derived in "Appendix 1"

Table 2 Model parameters and default values

Parameter	Value	Unit	Interpretation
β	100	–	Preferred predator–prey mass ratio
σ	1	–	Width of selection function
q	0.75	–	Exponent of volumetric search rate[a]
n	0.75	–	Exponent of maximum consumption rate
r	1	–	Exponent of maintenance
α	0.6	–	Assimilation efficiency[b]
m_b	0.001	g	Egg size[c]
M_0	1	g	Lower limit of trait value[c]
M_b	10^6	g	Upper limit of trait value[c]
μ_b	0.04	g^{q-1}	Scaled background mortality[d]
λ	$2+q-n$	–	Expected exponent of community size spectrum

Parameter values are from Andersen and Beyer (2006) except:
[a]Theoretically expected value is 0.8 (Andersen and Beyer 2006). Choosing 0.75 is to ensure constant food intake for offspring when varying β and σ ("Appendix 1")
[b]Hartvig et al. (2011)
[c]Empirical data reveals that individual body size spans 12 orders of magnitude (Cohen et al. 2003) including resource spectrum. Resource size is set from 0.001 to 1 mg, covering (zoo)plankton (Brooks and Dodson 1965). Egg size m_b is assigned 1 mg, consistent with the mass of newly hatched larvae corresponding to egg diameter of 1 mm (Chambers 1997). Asymptotic size is restricted to the range from $M_0 = 1$ g to $M_\mathrm{b} = 10^6$ g
[d]Adjusted to give a maximum individual size around 1 ton

The dynamical equation governing $N_\mathrm{c}(w,t)$ can in principle be obtained by integrating both sides of Eq. 1 over M

$$\frac{\partial}{\partial t}\int N(m,M,t)\mathrm{d}M = \int \frac{\partial}{\partial m}(g(m,M,t)N(m,M,t))\mathrm{d}M - \int \mu(m,t)N(m,M,t)\mathrm{d}M, \quad (3)$$

which gives rise to

$$\frac{\partial}{\partial t}N_\mathrm{c}(m,t) = \frac{\partial}{\partial m}\int (g(m,M,t)N(m,M,t))\mathrm{d}M - \mu(m,t)N_\mathrm{c}(m,t). \quad (4)$$

Clearly, the essence of deriving the community model is to evaluate the integral appearing in Eq. 4. To this end, we define $\tilde{g}_\mathrm{c}(m,t)$ by

$$\tilde{g}_\mathrm{c}(m,t)N_\mathrm{c}(m,t) = \int g(m,M,t)N(m,M,t)\mathrm{d}M \quad (5)$$

and rewrite Eq. 5 as

$$\frac{\partial}{\partial t}N_\mathrm{c}(m,t) = \frac{\partial}{\partial m}(\tilde{g}_\mathrm{c}(m,t)N_\mathrm{c}(m,t)) - \mu(m,t)N_\mathrm{c}(m,t). \quad (6)$$

$\tilde{g}_\mathrm{c}(m,t)$ can be perceived as the averaged growth rate of m-sized individuals, which is time-dependent through current food availability, i.e., $N_\mathrm{c}(m,t)$. Recalling that the somatic growth rate in the trait-based model is expressed as $g(m,M,t) = \varepsilon_I(m,M)E(m,t)$ and $E(m,t)$ is independent of trait M, we introduce an averaged growth efficiency $\tilde{\varepsilon}_I(m,t)$ over trait M defined by

$$\tilde{\varepsilon}_I(m,t)N_\mathrm{c}(m,t) = \int \varepsilon(m,M)N(m,M,t)\mathrm{d}M \quad (7)$$

and therefore $\tilde{g}_\mathrm{c}(m,t) = \tilde{\varepsilon}_I(m,t)E(m,t)$.

Apparently, $\tilde{\varepsilon}_I(m,t)$ varies with $N(m,M,t)$. To eliminate the dependence on $N(m,M,t)$ which is trait-dependent, we approximate $\tilde{\varepsilon}_I(m,t)$ with a trait-independent averaged growth efficiency $\tilde{\varepsilon}_I(m,t) \simeq \bar{\varepsilon}_I(m)$. Such an approximation can be found using the "metabolic" assumption that the consumption rate $E(m) \propto m^n$ on average, where $n = 3/4$. From this assumption, the trait-based model Eq. 1 can be solved completely to give an equilibrium solution (Andersen and Beyer 2006)

$$N_{eq}(m,M) \propto M^{2n-q-3+\frac{\alpha_p}{\alpha h}} m^{-n-\frac{\alpha_p}{\alpha h}} \times \left(1-\left(\frac{m}{M}\right)^{r-n}\right)^{\frac{\alpha_p}{\alpha h(r-n)}-1}, \quad (8)$$

where $\alpha_p = \gamma\kappa e^{(1+q-\lambda)^2\sigma^2/2}\beta^{1+q-\lambda}$. Inserted into Eq. 7, the equilibrium solution makes it possible to derive the following form of $\bar{\varepsilon}_I$ ("Appendix 2"):

$$\bar{\varepsilon}_I = a\alpha e^{(2n(q-1)-q^2+1)\sigma^2/2}/(2+q-2n), \quad (9)$$

which is neither size- nor trait-dependent but constant. Thus, $\tilde{g}_\mathrm{c}(m,t) \simeq g_\mathrm{c}(m,t) = \bar{\varepsilon}_I E(m,t)$, and the community model is then given as

$$\frac{\partial}{\partial t}N_\mathrm{c}(m,t) = \frac{\partial}{\partial m}(g_\mathrm{c}(m,t)N_\mathrm{c}(m,t)) - \mu(m,t)N_\mathrm{c}(m,t). \quad (10)$$

In this manner, only the growth efficiency is determined by the approximate solution of the model while the actual growth rate will still depend on the amount of encountered food. In other versions of the community model, the growth efficiency is set more or less arbitrarily (Benoît and Rochet 2004; Blanchard et al. 2009; Law et al. 2009; Datta et al. 2010; Plank and Law 2011), but the procedure given here for determining the growth efficiency from the trait-based model determines the value from basic principles. The community model is therefore similar to the trait-based model with the only exception that $N(m, M, t)$ is replaced by $N_c(m, t)$ and $\varepsilon_I(m, M)$ by $\bar{\varepsilon}_I$.

In summary, the trait-based model represents the trait diversity through the dependence of $N(m, M, t)$ on asymptotic body size M, while abundance in the community model (Eq. 10) only depends on size and therefore does not distinguish between any sort of species or life-history diversity. The advantage of deriving the community model from the trait-based model is that the two models are so similar that a direct comparison between them is possible. In this way, we have obtained the community model as a reduced version of the trait-based model where all information about trait diversity has been integrated out of the model. The key difference between the models is the difference in the growth of individuals with a given size. In both models, growth is food-dependent, but in the trait-based model, individuals of a given size will have different growth rates depending on their trait values, while all individuals of a given size will grow with the same rate in the community model.

Model implementation

An appropriate scaling of time and density can reduce the effective number of parameters in the models. Three-dimensional parameters are under consideration: the factor of the volumetric search rate γ (weight^{-q}volume/time), resource spectrum magnitude κ (weight$^{\lambda-1}$/volume), and background mortality μ_b (1/time). γ represents individual foraging ability while κ the food availability for small individuals that further serve as food items for large individuals. Scaling Eq. 1 by setting $\tilde{N}(m, M, t) = N(m, M, t)/\kappa$ and $\tilde{t} = t\kappa\gamma$ makes it possible to eliminate γ and κ from system by defining a scaled background mortality $\tilde{\mu}_b = \mu_b/(\gamma\kappa)$. Equation 10 and the resource spectrum are scaled analogously. The maximum size M_b can be approximated as the size where the background mortality equals the expected predation mortality $M_b \sim \tilde{\mu}_b^{1/(q-1)}$. Given an appropriate value of $\tilde{\mu}_b$, M_b is accessible. The main relevant parameters are therefore the parameters describing selection of food, i.e., β and σ. To suppress excessive notation, the tildes of the scaled variables are dropped and the time variable t is ignored in the following.

To find the equilibrium solution of both models, individual and asymptotic body sizes are divided into discrete individual size groups and trait groups. The partial differential equations (PDEs) 1 and 10 are discretized using the upwind semi-implicit scheme (Hartvig et al. 2011). This discretization transforms the PDEs into a system of ordinary differential equations (ODEs). Equilibrium solutions are found using Newton's parameter continuation ("Appendix 3"). The stability of the equilibrium solution is determined by the maximum real part (ρ_{max}) of the eigenvalues of the Jacobian matrix for the system of ODEs ("Appendix 3"). If ρ_{max} is negative, then the equilibrium is stable and vice versa. The non-equilibrium solutions are found by numerical integration of the ODEs ("Appendix 3"). Even though all processes in the models are individual-based, the scaling using Eqs. 1 and 10 lifts the level from individual to community. Using the numerical solution procedure, the models can be integrated forward reliably.

Results

The equilibrium solution of the two models conforms the theoretical scaling solution for $m \ll M_b$ (Fig. 1). When the size approaches M_b, the background mortality dominates over the predation-induced mortality and the spectra converge toward zero. The convergence happens faster in the trait-based model than in the community model. This is due to the reduction of the growth rates of the largest individuals in the trait-based model as they approach their asymptotic size (Fig. 2a). The growth rates of individuals with intermediate sizes (i.e., $m \ll M_b$) in the community model are in fairly good agreement with the average growth rates in the trait-based model and also conforms well with the theoretically expected growth rate. The distribution of growth rates in the trait-based model is also in accordance to the theoretically expected distribution (Fig. 2b). For the very largest individuals, there is a discrepancy between the two models, as there is no mechanism to slow down growth in the community model. All in all, the equilibrium solutions of the size spectra of the two models are fairly similar, and the discrepancies can be traced to the fundamental differences in the growth trajectories of individuals, as expected.

The stability analysis of the equilibrium size spectrum demonstrates that ρ_{max} obtained from the trait-based model is in general smaller than the community

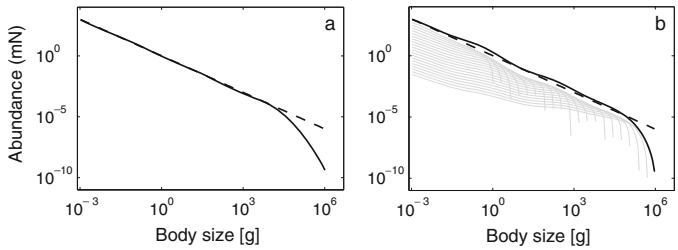

Fig. 1 Equilibrium community size spectrum (*solid*) in the community model (**a**) and in the trait-based model (**b**) *under* default parameter values (Table 2). *Dashed lines* are the theoretically expected community biomass size spectrum, i.e., $\overline{N}_c(m) = m^{-\lambda}$. The *gray curves* indicate species size spectra, the summation over which gives rise to the community size spectrum (i.e., $N_c(m) = \sum_j N(m, M_j)$)

model (Fig. 3), implying that the equilibrium of the trait-based model is more stable than the community model. In particular, there is a region of σ and β where the equilibrium size spectrum is stable in the trait-based model but unstable in the community model. Although the parameter range where this occurs is rather limited, it is just around the default values of σ and β. Increasing diet breadth σ or decreasing the preferred predator–prey mass ratio β decreases $\rho_{\max}$, suggesting that a diet consisting of a wide size-range of individuals close to the size of the predator tends to stabilize community dynamics.

To examine the influences of trait diversity on the non-equilibrium solutions, of the two size-spectrum models, we focus on a parameter range where the equilibrium solutions of both models are unstable, namely $\beta = 100$ and $\sigma = 1$. This leads to an oscillating solution with traveling waves moving up in size with increasingly large amplitude (see Benoît and Rochet 2004; Law et al. 2009).

The time averages of the oscillating solutions of both models are very similar to the equilibrium solutions for the small sizes (Fig. 4). There is some deviation between the equilibrium solutions and the average solutions, in particular for the community model. For both models, the amplitudes of the oscillations are increasing with size, but the amplitude is much larger in the community model than in the trait-based model. As the size approaches the maximum size M_b, the oscillations are diminishing in amplitude. The dynamics is therefore more extreme in the community model than in the trait-based model.

To have a closer look at the nature of the oscillations around the equilibrium solution, we focus on two particular individual sizes with a size ratio equal to the preferred predator–prey mass ratio (Fig. 5) to compare with the type of oscillation observed in two species predator–prey models like the Lotka–Volterra predator–prey model. Here, again, the equilibrium and the average solution are fairly close to one another,

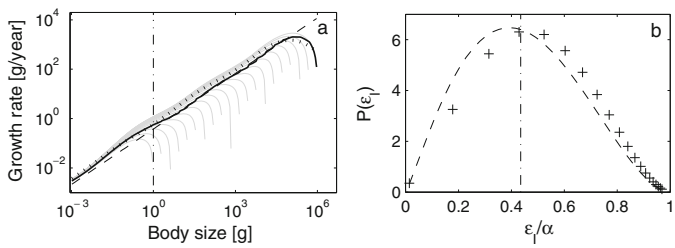

Fig. 2 Individual growth rate (**a**) and the distribution of growth rate for individuals of size $m = 1$ g (*vertical dash-dotted line*) (**b**) calculated from the equilibrium solution corresponding to Fig. 1. In **a**, the average growth rate (*solid black*) is obtained through $g_c(m) = \sum(g(m, M_j)N(m, M_j))/\sum N(m, M_j)$, where $g(m, M_j)$ are individual growth rates within species M_j (*gray*). The *dotted and dashed curves*, respectively, indicate the individual growth rates in the community model and the theoretically expected average growth rate, i.e., $g_c(m) = \overline{\varepsilon}_I \kappa \gamma m^n$. In **b**, for given individual size 1 g, the theoretically expected (*dashed*) and realized (*plus sign*) distributions of individual growth efficiency $P(\varepsilon_I)$ are presented. The *vertical dash-dotted line* indicates the theoretically expected average growth efficiency $\overline{\varepsilon}_I$

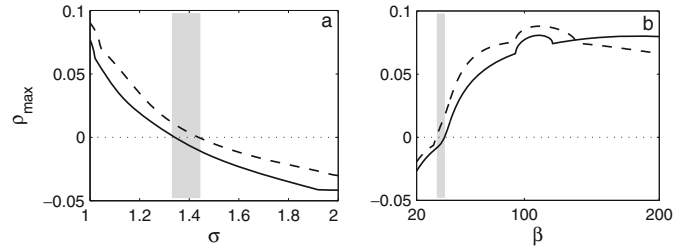

Fig. 3 Maximum real part (ρ_{max}) of the eigenvalues of the equilibrium size spectrum in the community model (*dashed*) and in the trait-based model (*solid*) as functions of the diet width σ **a** and the preferred predator–prey mass ratio β **b**. The *gray* bands illustrate the parameter regions where the equilibrium solution is stable in the trait-based model but unstable in the community model. Other parameter values are kept the same as in Table 2

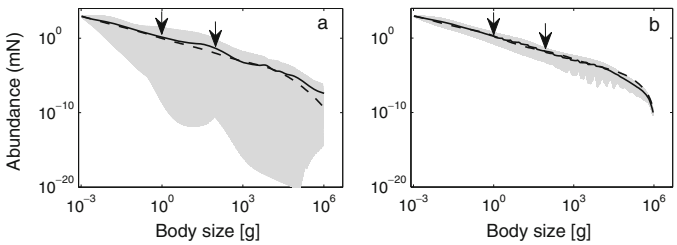

Fig. 4 The time-average spectrum (*solid*) and the equilibrium size spectrum (*dashed*) in the community model (**a**) and in the trait-based model (**b**), respectively. *Shaded areas* show the oscillating regions of the time-series. Parameter vales are chosen from Table 2 which destabilizes the equilibrium solution in both models. *Arrows* indicate the individual sizes $m_1 = 1$ g and $m_2 = 100$ g that are used in Figs. 5, 6, and 7

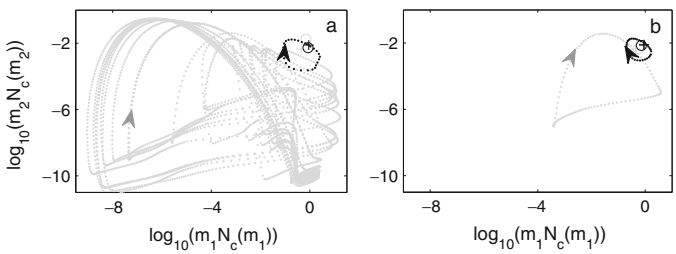

Fig. 5 Base ten logarithm of the total abundance of individuals $m_1 = 1$ and $m_2 = 100$ in the community model (*gray*) and in the trait-based model (*black*), respectively. *Circle* and *plus sign*, respectively, indicate the time-averaged and the equilibrium solutions. *Arrows* show the direction of motion. *Dots* are plotted every 0.04 years in the community model while 0.4 years in the trait-based model. A striking observation is that predator–prey phase portrait changes from a chaotic state to a periodic state in the community model as σ is increased from 1 (**a**) to 1.2 (**b**). Other parameter values are the same as in Fig. 4

but the oscillations in the community model are much larger than in the trait-based model, and the community model may even show chaotic solutions for small values of σ. The solutions are revolving clockwise around the equilibrium in a limit cycle, which is the opposite direction than in the Lotka–Volterra predator–prey model. The reason is that the phase shift between the two populations is not governed by population growth as in the Lotka–Volterra predator–prey model but rather by the lag induced by the time it takes for a prey to grow to predator size. The rate of change of predator and prey populations is not constant and particularly slow at low abundances, in particular for the community model. Therefore, the typical situation in the community model is that the population for a given size range is almost extinct interspersed by periods of very high abundance.

The time series of individual abundance (Fig. 6) further reveal that in the trait-based model, the abundance of individuals having the same body size (100 g) but different trait M_j has the same frequency but different phases. This variation of the phases between individuals of the same size but different trait value is responsible for the small amplitude of the total population abundance ($\sum 100N(100, M_j)$) as the dynamics of individuals with different trait values tend to cancel out each other. The variation between phases is a result of the different growth rates between species, which cannot occur in the community model.

A frequency analysis of the predator–prey dynamics of the two models largely confirms the previous observations (Fig. 7), namely that the amplitude of the oscillation is larger in the community model than in the trait-based model. It also shows that the community model excites many more frequencies than the trait-based model where the dynamics is dominated by one basic frequency. The dynamics of the trait-based model is therefore much closer to a linear dynamics whereas the dynamics of the community model is fully non-linear.

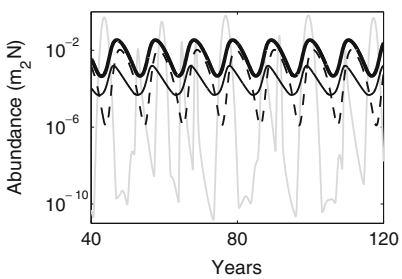

Fig. 6 Time series of individual abundance with particular body size $m_2 = 100$ but with different trait values: $\sum m_2 N(m_2, M_j)$ (*thick solid*), $m_2 N(m_2, M_j = 200)$ (*dashed*), $m_2 N(m_2, M_j = 20{,}000)$ (*thin solid*). *Gray curve* represents the community model while *black ones* represent the trait-based model. Parameter values are the same as in Fig. 4

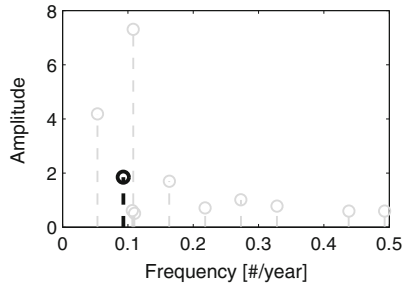

Fig. 7 Distribution of wave frequency built in the time series of individual abundance $m_2 N_c(m_2, t)$ in the community model (*gray*) and in the trait-based model (*black*), where $m_2 = 100$. *Y*-axis indicates the approximated amplitudes of $\log_{10}(m_2 N_c(m_2, t))$. Frequencies are decomposed using the Fourier transformer and presented only with amplitudes greater than 0.5. Parameter values are the same as in Fig. 4

Discussion

We have systematically explored the differences in equilibrium stability and non-equilibrium dynamics between two models of marine communities where the dominant mode of trophic transfer of energy is through the growth of individuals. The study of size-spectrum models offers a very different view on both community dynamics and on the question of stability of communities than that offered by food-web models. By ignoring all aspects of the interactions between specific species, it is possible to focus on the interactions between individuals only and to make a more general and complete analysis than are possible by food-web models. This does not mean that the size-spectrum models will replace current food-web models but rather that they form a valuable complementary modeling approach. The two size-spectrum models examined here differ in whether life-history diversity is included or not. The community model treats all individuals of a given size as being equal, whereas the trait-based model distinguishes between individuals with different trait values, here asymptotic size. This difference makes it possible, in a very clean manner, to examine the importance of trait diversity on community dynamics

The equilibrium solutions of the two models are largely similar and confirm the theoretical predictions of a scaling community size spectrum (Benoît and Rochet 2004; Law et al. 2009). This demonstrates

that we have solved the models correctly and that we have set up the two models to be as similar as possible to facilitate a comparison.

A stability analysis is used to examine whether the equilibrium solutions will be stable or not. We found that both stable and unstable solutions were possible. Reducing preferred predator–prey mass ratio (β) and increasing diet width (σ) contribute to stabilize the size spectrum. This finding is in accordance with other stability analyses of the community model (Datta et al. 2010, 2011; Plank and Law 2011). The stabilizing effect of increasing the diet width is in accordance with the results from food-web theory that more weak links make the food webs more likely to have stable equilibria (May 1972; McCann et al. 1998). The important novel finding is that trait diversity increases the region of parameter space with stable solutions, and it generally decreases the strength of the instability (lower maximum real eigenvalue). The stabilizing mechanism is the difference in growth between individuals in the trait-based model. Another stabilizing effect was seen in the jump-growth master equation, which is similar to the standard McKendric–von Foerster equation employed here (Law et al. 2009). The deterministic jump-growth community model is obtained as a limit of the stochastic predation-growth process where individuals experience jumps in body size as they consume smaller organisms (Datta et al. 2010). The equilibrium solution of the jump-growth model is more stable than the community model (Datta et al. 2011), and it was shown that the standard community model is actually the first-order approximation of the jump-growth equation. Looking at the second-order approximation, i.e., the McKendric–von Foerster equation with diffusion, the diffusion term in growth rate tends to stabilize size spectrum by making the real part of eigenvalue more negative typically for large wave number (Datta et al. 2011). Even though these results from the analysis of the jump-growth equation also indicate that differential growth rates between individuals have stabilizing effect, the basic mechanism is fundamentally different from the one introduced in the trait-based model. In the trait-based model, the difference in growth rates is explicitly due to individuals having different traits, which is similar to individuals belonging to different species, whereas the jump-growth model resolves differences due to the discrete process of food consumption (food chunks have a finite size), which is akin to the effect of demographic noise.

The classic Lotka–Volterra predator–prey model possesses the mathematical property that the time average of periodic population abundance equals the value at the marginally stable equilibrium (Hofbauer and Sigmund 1988). This averaging property also holds for almost-periodicity solutions to a more general class of bi-linear food-web models (Law and Morton 1993), which motivates interest in the equilibrium, whether it is stable or not. In contrast, the two size-spectrum models do not have the bi-linear form of a Lotka–Volterra model, so there is no theoretical reason to expect the averaging property to hold. We have explored the difference between the equilibrium and averaged solutions of the two size-spectrum models numerically. For both models, the time average of non-equilibrium solutions is quite close to the equilibrium value, even if the two do not match exactly. The results indicate that the equilibrium solution might be a good approximation to the average of the non-equilibrium solutions, and even if this conclusion is mathematically imprecise, it may justify interest in the equilibrium properties of size-spectrum models.

The non-equilibrium dynamics of the two models are qualitatively similar with waves travelling up through the size classes until they are dissipated at the highest sizes. However, the amplitude and frequency of the oscillations differ. The community model has faster and much more violent oscillations than the trait-based model, and it even possesses seemingly chaotic solutions. The oscillations in the trait-based model are close to sinusoidal which indicates that the dynamics is only weakly non-linear. This gives hope that it will be possible to treat the model as a pattern forming system and derive a weakly non-linear expansion around the bifurcation point in the form of an amplitude equation (Cross and Hohenberg 1993). Such a simplified model would make more analytical work possible.

In conclusion, we have shown how the trait diversity of the trait-based model leads to both increased stability of equilibrium solutions to the modeled community as well as much more regular non-equilibrium dynamics than the community model. We have only examined the effect of including one life history trait, and it may be argued that the effect we have demonstrated is merely an artifact of this particular trait and that other traits may have a different effect. We have demonstrated how the increase in stability is due to the distribution in growth rates among individuals with the same size. Introducing other traits is likely to have a similar effect on growth rates, even though the specific mechanism may be different, and therefore, we expect that using other traits, or additional traits, will have a similar stabilizing effect. It should be kept in mind that the trait-based model differs from a food-web framework in two aspects: The reproduction is specified by a constant renewal rate, and there is no species preference. To make a full food-web framework with ontogenetic

trophic niche shifts, both of these aspects have to be taken into account (Hartvig et al. 2011). Nevertheless, our results demonstrate that taking individual life history into consideration will lead to qualitative changes in the dynamical properties, compared to the results of the community model. Therefore, conclusions of the dynamical properties of marine ecosystems that are based on the community models (e.g., Benoît and Rochet 2004; Law et al. 2009; Rochet and Benoît 2011) should be reconsidered. However, the predictions of the equilibrium solution and the average of the dynamical solution of the community model are still valid. We finally conclude that in ecosystem dominated by individuals with ontogenetic trophic niche shifts, increased diversity and complexity lead to increased stability of the ecosystem.

Acknowledgements Ken Haste Andersen acknowledges financial support from EU FP7 project FACTS. Martin Hartvig is kindly acknowledged for helpful discussions. We greatly thank the reviewers for constructive comments on this paper.

Appendix 1: Boundary condition

We derive the lower boundary condition $N(m_\mathrm{b}, M)$ in the trait-based model on the basis of equilibrium size spectrum (ESS) theory (Andersen and Beyer 2006). Moreover, we assume that the total offspring recruitment in the trait-based model equals the recruitment in the community model, that is,

$$\int_{M_0}^{M_\mathrm{b}} N(m_\mathrm{b}, M)\mathrm{d}M = \kappa m_\mathrm{b}^{-\lambda}. \tag{11}$$

The ESS theory involves two assumptions. On one hand, the community size spectrum is of a power law state, that is, $\overline{N}_\mathrm{c}(m) = \kappa m^{-\lambda}$. On the other hand, the feeding level, indicating the mount of energy routed to individual somatic growth, is constant. Under these two conditions, Andersen and Beyer (2006) found the analytical solution to Eq. 1

$$\overline{N}(m, M) = k_0 M^{2n-q-3+a} m^{-n-a}\left(1-\left(\frac{m}{M}\right)^{r-n}\right)^{\frac{a}{r-n}-1}, \tag{12}$$

where $a = \beta^{2n-q-1}/\alpha$ is the physiological predation rate and k_0 a constant satisfying $\int_m^\infty \overline{N}(m, M)\mathrm{d}M = \kappa m^{-\lambda}$. The exponent of community size spectrum is found to be $\lambda = 2 + q - n$. Due to Eq. 11, the lower boundary condition is set as

$$N(m_\mathrm{b}, M) = f_0 \overline{N}(m_\mathrm{b}, M)/k_0 \simeq f_0 M^{2n-q-3+a} m_\mathrm{b}^{-n-a}. \tag{13}$$

Therefore, f_0 is calculated by evaluating

$$f_0 = k_0 \kappa m_\mathrm{b}^{-\lambda+n+a} / \int_{M_0}^{M_\mathrm{b}} \overline{N}(m_\mathrm{b}, M)\mathrm{d}M. \tag{14}$$

Since resource spectrum is fixed, encountered food of offspring can be calculated analytically

$$\begin{aligned} E(m_\mathrm{b}) &= \gamma m_\mathrm{b}^q \int_{10^{-6}}^{10^{-3}} \kappa w^{1-\lambda}\varphi(m_\mathrm{b}/w)\mathrm{d}w \\ &\simeq \gamma m_\mathrm{b}^q \int_0^\infty \kappa w^{1-\lambda}\varphi(m_\mathrm{b}/w)\mathrm{d}w \\ &= \gamma\kappa\beta^{\lambda-2} e^{(\lambda-2)^2\sigma^2/2} m_\mathrm{b}^{2+q-\lambda}. \end{aligned}$$

Note that $\lambda = 2$ when $q = n$. Thus, $E(m_\mathrm{b})$ is independent of the width of selection function σ and the preferred predator–prey mass ratio β.

Appendix 2: Averaging growth efficiency

The average of growth efficiency is calculated based on the ESS theory, and our calculation is in principle a replicate of Andersen and Beyer (2006) and Andersen et al. (2009). In order for completeness, we present it here briefly.

The ESS theory assumes an infinite size range for community size spectrum, i.e., $\overline{N}_\mathrm{c}(m) = km^{-\lambda}$, $0 < m < \infty$. The advantage is that we can get a closed form when doing integration to obtain individual encountered food (Eq. 15) and mortality (Eq. 18), whereas in our trait-based model and community model, size spectrum is, however, truncated for numerical calculations. The individual encountered food can be calculated as

$$E(m) = \gamma m^q \int_0^\infty w\overline{N}_\mathrm{c}(w)\varphi(m/w)\mathrm{d}w = \kappa\alpha_e m^n, \tag{15}$$

where $\alpha_e = \gamma\beta^{\lambda-2}e^{(\lambda-2)^2\sigma^2/2}$. Thus, individual somatic growth rate is

$$g(m, M) = \alpha\left(1-\left(\frac{m}{M}\right)^{r-n}\right)E(m). \tag{16}$$

According to Eqs. 12 and 16, the average growth rate is calculated as

$$g_\mathrm{c}(m) = \frac{1}{\overline{N}_\mathrm{c}}\int_m^\infty g(m, M)\overline{N}(m, M)\mathrm{d}M = \alpha_\mathrm{c} m^n, \tag{17}$$

where the coefficient α_c is to be determined.

The mortality rate is

$$\mu(m) = \int_0^\infty \gamma w^q \overline{N}_\mathrm{c}(m)\varphi(w/m)\mathrm{d}w = \alpha_p m^{1+q-\lambda}, \tag{18}$$

where $\alpha_p = \gamma\kappa e^{(1+q-\lambda)^2\sigma^2/2}\beta^{1+q-\lambda}$. Inserting the average growth rate (Eqs. 16 and 18) into the stationary equation of Eq. 10, we obtain

$$\frac{\partial}{\partial m}(N_c(m)g_c(m)) = \mu(m)N_c(m). \tag{19}$$

By solving the equation (Eq. 19), the exponent of the community size spectrum is found to be $\lambda = n + \alpha_p/\alpha_c$. Notice that $\lambda = 2 + q - n$, and then $\alpha_c = \alpha_p/(2 + q - 2n)$.

Dividing Eqs. 17 by 15, the average growth efficiency is

$$\bar{\varepsilon}_I = \frac{\beta^{2n-q-1}}{2+q-n}e^{((n-1)^2-(q-n)^2)\sigma^2/2}. \tag{20}$$

Appendix 3: Tracing equilibrium and determining stability

To solve the non-equilibrium dynamics to the trait-based size-spectrum model, we refer readers to Hartvig et al. (2011) where detailed numerical program is included and the key point is how to discretize the McKendrick–von Foerster equation which is presented in Eq. 21. Analogously, the dynamics of the community size spectrum can also be solved. In the following, the focus is how to continuously trace equilibrium solution as a function of a free parameter (e.g., the diet width σ). To this end, we apply Newton's parameter continuation (Kuznetsov 1994) combined with the semi-implicit upwind scheme (Hartvig et al. 2011). Since body size spans several orders of magnitude, logarithmical size is preferred. Details of the logarithmical transformation can be referred to Benoît and Rochet (2004). We describe our technical approach by taking the community model as an example.

Discretization

Set $x = \log(m)$ and discretize x as $x_i = \log(m_b) + \Delta x, i = 0, \cdots, k$, where $x_k < \log(M_b) < x_{k+1}$. In addition, let $u_i^t = u(x_i, t)\Delta x = N(m(x_i))m(x_i)\Delta x$ represent the total number of individuals in the range of $[x_{i-1}, x_i]$. Then the discretization of the McKendrick–von Foerster Eq. 10 can be described as follows:

$$\frac{u_i^{t+\Delta t} - u_i^t}{\Delta t} = -\frac{g_i^t u_i^{t+\Delta t} - g_{i-1}^t u_{i-1}^{t+\Delta t}}{\Delta x} - \mu_i^t u_i^{t+\Delta t}, \tag{21}$$

where

$$g_i^t = \bar{\varepsilon}_I \gamma e^{(q-1)x_i}\sum_j e^{x_j}u_j^t\varphi(x_i - x_j), \tag{22}$$

and

$$\mu_i^t = \gamma\sum_j e^{qx_j}u_j^t\varphi(x_j - x_i). \tag{23}$$

Set $U^t = (u_1^t, \cdots, u_k^t)'$, $B = (\frac{\Delta t}{\Delta x}g_0u_0, 0, \cdots, 0)'$, where the subscript indicates the transpose of a matrix or a vector. g_0 is completely determined by the resource spectrum and thus constant.

Equation 21 has an equivalent form

$$A(U^t)U^{t+\Delta t} - U^t - B = 0, \tag{24}$$

where $A(U)$ is a do-bidiagonal matrix and along the main and lower diagonals are vectors $a = (a_i)$ and $b = (b_i)$, respectively. Moreover, the entries in these two vectors are

$$a_i = 1 + \frac{\Delta t}{\Delta x}g_i^t + \Delta t\mu_i^t \tag{25}$$

and

$$b_i = -\frac{\Delta t}{\Delta x}g_i^t. \tag{26}$$

Set $F(U) := A(U^t)U^{t+\Delta t} - U^t - B$. Making an explicit dependence of F on the free parameter leads to

$$F(U, \sigma) = 0. \tag{27}$$

Newton's continuation

Now it is ready to perform the Newton's continuation using Eq. 27. Detailed description is referred to Kuznetsov (1994). We here present how to calculate the Jacobian matrix of Eq. 27 for given equilibrium U and σ.

Define $\mathrm{d}F\mathrm{d}U$ to be the Jacobian matrix, which is of k^2 dimension, and set c_j to be a row vector of dimension k whose entries are all zero except for the j-th component which is exactly 1. The $\mathrm{d}F\mathrm{d}U$ can be calculated as follows: Noticing the special structure of the matrix $A(U)$, the first row of the Jacobian is

$$\mathrm{d}F\mathrm{d}U(1,:) = \left(\frac{\Delta t}{\Delta x}\frac{\mathrm{d}g_1}{\mathrm{d}U} + \Delta t\frac{\mathrm{d}\mu_1}{\mathrm{d}U}\right)u_1 + (a_1 - 1)c_1, \tag{28}$$

and for $j > 1$

$$\mathrm{d}F\mathrm{d}U(j,:) = -\frac{\Delta t}{\Delta x}\frac{\mathrm{d}g_{j-1}}{\mathrm{d}U}u_{j-1} + b_{j-1}c_{j-1} + \left(\frac{\Delta t}{\Delta x}\frac{\mathrm{d}g_j}{\mathrm{d}U} + \Delta t\frac{\mathrm{d}\mu_j}{\mathrm{d}U}\right)u_j + (a_j - 1)c_j, \tag{29}$$

where $\mathrm{d}g_j/\mathrm{d}U$ and $\mathrm{d}\mu_j/\mathrm{d}U$ are row vectors with the following form:

$$\frac{\mathrm{d}g_j}{\mathrm{d}U} = \bar{\varepsilon}_I \gamma e^{((q-1)x_j)}[e^{x_1}\varphi(x_j - x_1), \cdots, e^{x_k}\varphi(x_j - x_k)], \tag{30}$$

$$\frac{\mathrm{d}\mu_j}{\mathrm{d}U} = \gamma[e^{qx_1}\varphi(x_1 - x_j), \cdots, e^{qx_k}\varphi(x_k - x_j)]. \tag{31}$$

To calculate the derivative of F with respect to the free parameter, we use the forward finite difference as an approximation, i.e.,

$$\mathrm{d}F\mathrm{d}\sigma = (F(U, \sigma + \delta) - F(U, \sigma))/\delta, \tag{32}$$

where $\delta = \max\{\sigma\delta_1, \delta_2\}$.

Implementation of the parameter continuation in the trait-based model is similar but more challenging. Apart from the discretization along the direction of individual body size, the trait is also discretized evenly on the logarithmical scale. Thus, the matrix in Eq. 24 is now a black don-bidiagonal of K^2 dimension with $K = \sum_{i=1}^{L} k_i$, where k_i is the number of discretized points for species i and L is the number of discretized species. Each block matrix has the same structure as the matrix in Eq. 24 with entries Eqs. 25 and 26.

After some initial experimentation, we found that setting $\Delta x = 0.1, \Delta t = 0.02, \delta_1 = 10^{-4}, \delta_1 = 10^{-7}, L = 20$ could produce reliable result without causing too much computational effort, even though the precise choice of discretization affects the resolution of the approximation.

Determining the stability of equilibrium

In analogy to Eq. 21, discretization of the McKendric–von Foerster equation at given equilibrium U gives rise to

$$\frac{\partial}{\partial t}u_i(t) = -\frac{g_i u_i - g_{i-1}u_{i-1}}{\Delta x} - \mu_i u_i, \tag{33}$$

where g_i and μ_i are similar with Eqs. 22 and 23. Rewriting the right-hand side of Eq. 33 as a matrix leads to

$$G(U) = A_\mathrm{s}(U) + B_\mathrm{s}, \tag{34}$$

where A_s and B_s are similar to A and B but the entries are $-\frac{a_i - 1}{\Delta t}$ and $-\frac{b_i}{\Delta t}$ in A_s and $B/\Delta t$ in B_s. The Jacobian matrix of $G(U)$ with respect to U can be calculated in analogy to Eqs. 28 and 29. Stability of equilibrium U is determined through the maximum real part of the Jacobian matrix of $G(U)$ with positive value meaning unstable and vice versa.

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Paper IV

Four types of interference competition and their impacts on the ecology and evolution of size-structured populations and food webs

Zhang L., Andersen K.H., Dieckmann U., Brännström Å., 2011. Four types of interference competition and their impacts on the ecology and evolution of size-structured populations and food webs (*manuscript*).

Four types of interference competition and their impacts on the ecology and evolution of size-structured populations and food webs

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Abstract

Theoretical description of evolutionary speciation has generally been considered using unstructured population models. In this paper, we explore the conditions necessary for speciation in a continuously size-structured population model with a single evolving trait describing size at maturation. As interference can take different forms in size-structured population models, contrasted with the only mortality form in unstructured population models, four types of interference are modeled and examined systematically, namely interference in foraging, metabolism, survival, and recruitment. On the one hand, although all types of interference reduce population biomass, adult abundance (survival interference) and reproduction rate (survival and recruitment interference) could be increased, when interference induced gain exceeds the cost. On the other hand, impacts of interference on maturation size and communities vary with underlying mechanisms. In monomorphic population environment size at maturation is either depressed (foraging and metabolism interference) or elevated (survival and recruitment interference), although the disruptive strength at equilibrium maturation size is enhanced by all interference mechanisms. While foraging and recruitment interference are more liable to induce the initial diversification, only survival interference

is able to produce large communities with complex trophic structure. Moreover, there is no clearly positive relationship between the initial and the final diversification, and species-richer food webs do not necessarily have higher trophic level.

Keywords: Adaptive dynamics, biodiversity, evolutionary branching, size-structured population modeling

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1. Introduction

Species diversity has considerable impacts on ecosystem functioning (Tilman, 1996; Naeem and Li, 1997; Borrvall et al., 2000; Ives et al., 2000; Ives and Carpenter, 2007). To explore the impacts, ecological communities are constructed in many different ways but in general represented as food webs by considering the trophic interactions between species with different forms of interaction matrices (Cohen et al., 1990; Solow and Beet, 1998; Williams and Martinez, 2000; Cattin et al., 2004). Although the structure and stability of the community networks can be delineated successfully, such approaches, using some emergent community properties to investigate others, cannot describe the gradual development of food webs (Loeuille and Loreau, 2005; Brännström et al., 2010).

Two alternative approaches have recently been proposed to demonstrate the emergence of food webs. One is the ecological community assembly, which essentially describes the process of infrequent migration of species from the mainland (or species pool) to an island (Drake, 1990; Law and Morton, 1996; Morton and Law, 1997). The other is the evolutionary community assembly where a mutant emerges with a trait similar to its parent. Trait values of mutants are either chosen randomly in a vicinity of their parent trait values (Loeuille and Loreau, 2005) or deterministically resolved via canonical equations (Dieckmann and Law, 1996). During each process, coexistence and extinction are determined by ecological interactions (e.g. predation, competition) between the invading (or mutant) and the resident species, and a structurally stable food web is able to be developed gradually.

While a great number of work has been done on the evolutionary emergence of unstructured food-web models (e.g. Caldarelli et al., 1998; Drossel et al., 2001; Loeuille and Loreau, 2005; McKane, 2004; Rossberg et al., 2008; Brännström et al., 2010), there are very limited results on structured population models. Available results are restricted to models with

single size-structured species (Claessen and Dieckmann, 2002; Taborsky et al., 2003; Gårdmark and Dieckmann, 2006). In structured populations models, intrapopulation individuals are not indistinguishable in their physiological state any longer. Virtually, individual physiological state varies over the course of its life history, accompanied with changes in ecological performance (Werner and Gilliam, 1984). Food-dependent life history, as modeled in the physiologically size-structured population models (de Roos and Persson, 2001) and in the trait-based size-structured population model (Hartvig et al., 2011), has been demonstrated to have significant impacts on both population and community dynamics (de Roos et al., 2003), e.g. exciting alternative steady states (Claessen and de Roos, 2003), and resulting in catastrophic collapses of top predator (de Roos and Persson, 2002). However, it remains unclear how individual life history affects the evolutionary dynamics of food webs.

Unlike the physiologically size-structured population models whose parameters are species-based, the trait-based size-structured model avoids dealing with specific species by characterizing species by traits (e.g. size at maturation), and can be seen as a generalization of the former structured population mdoel. It can be applied not only at species levels (e.g. Zhang et al., 2011), but also at community levels (Andersen and Beyer, 2006; Andersen and Pedersen, 2010). To study the evolutionary dynamics of size-structured populations and food webs, we refine this model by introducing interference competition that takes pace between individuals with similar traits and similar body sizes.

Interference is ubiquitous among individual interactions (Case and Gilpin, 1974; Schoener, 1983) and generally viewed as a major force driving natural selection (Diamond, 1978; Schoener, 1982). Its significance has been demonstrated in understanding population behaviors (Carothers and Jaksic, 1984; Briffa and Sneddon, 2007; Nakayama and Fuiman, 2010), species coexistence (Vance, 1984; Amarasekare, 2002; Saito and Miki, 2010) and community biodiversity (Tilman, 1994; Adler and Mosquera, 2000; Loeuille and Loreau, 2005; Brännström et al., 2010). However, interference is usually represented as a single form of mortality in unstructured models, in stark contrast with its diverse mechanisms. In addition, interference occurs between engaged individuals rather than species. It is, therefore, desirable to model interference at the individual level. Here four mechanisms of interference are taken into consideration: reduction in the rates of foraging and recruitment, and increase in metabolism costs and mortality rate, respectively.

The goal of this paper is to understand, from the evolutionary point of view, how various interference mechanisms contribute to species diversity in a size-structured population model. To this end, we follows steps below: (1) Developing the four types of interference competition at the individual level in the trait-based size structured population model; (2) Investigating the impacts of interference on the demographic properties including population biomass, abundance and reproduction rate; (3) Exploring the effects of interference on the evolution of size at maturation; (4) Clarifying the relationship between the initial and final diversifications of evolved communities that are formed using evolutionary community assembly.

2. Ecological population dynamics without interference

The size-structured population model used in this paper is almost identical with the food-web framework in Hartvig et al. (2011). The only difference is that we do not assign a preference of any one species towards others. Brief model description goes as follows while the details including model equations and parameters are deferred to Appendix A

The model is on the basis of individual-level processes and species i are characterized by a trait, here size at maturation m_i (all sizes are given in terms of gram). An individual has two indices: a trait value to identify its species taxonomy, and a body size w to indicate its physiological state. Predation is the sole force driving individual growth and completely size based following the role of "big-eat-small". Scaling from individual-level processes to the population-level dynamics is described by the Mckendrick-von Foerster equation (McKendrick, 1926; von Foerster, 1959)

$$\frac{\partial}{\partial t}N_i(w,t) + \frac{\partial}{\partial w}(g_i(w)N_i(w,t)) = -\mu_i(w)N_i(w,t), \tag{1}$$

where $N_i(w,t)$ (or simply denoted by N_i) is the size spectrum of species m_i. The size spectrum describes the density distribution of individual (number of individuals per mass per volume) as a function of body size (Andersen and Beyer, 2006). $g_i(w)$ is the somatic growth rate of w-sized individuals of species m_i, which is food-dependent. Food comes from the size-based predation on both resource and consumer indivdiauls. Growth ceases when individuals reach the maximum body size $M_i = m_i/\eta$, i.e. $g_i(M_i) = 0$. Growth trajectory is biphasic where juveniles grow almost allometrically while adults follow the von Bertalanffy growth curve, as advocated by Lester et al. (2004).

$\mu_i(w)$ is the mortality rate consisting of predation by larger individuals, background death rate, and starvation in case of insufficient food to cover metabolic costs.

The boundary condition of equation (1) is formulated by the reproduction from adult individuals

$$g_i(w_0)N_i(w_0,t) = \frac{\varepsilon}{2w_0}\int_{w_0}^{M_i} b_i(w)N_i(w,t)dw, \tag{2}$$

where w_0 is the size of offspring that is assumed to be the same for all species. $b_i(w)$ is the food-dependent birth rate and ε is the reproduction efficiency. The fraction $1/2$ assumes equal sex distribution among individuals. The right-hand side of equation (2) represents the total flux of offspring. Inclusion of the juveniles into the integral is for mathematical convenience but their contribution to reproduction is zero.

Resource dynamics $R(w,t)$ is described using semi-chemostatic growth

$$\frac{d}{dt}R(w,t) = r_0 w^{n-1}(\kappa_0 w^{-\lambda} - R(w,t)) - \mu_p(w)R(w,t), \tag{3}$$

where $r_0 w^{n-1}$ is size-dependent growth rate (Savage et al., 2004). κ_0 and λ are the magnitude and slope of resource carrying capacity. $\mu_p(w)$ is the predation mortality imposed by consumer individuals. The sizes of resource organisms are confined to a finite range with an upper limit m_{cut}, whereas the lower limit is not crucial as long as it is far smaller than w_0.

In our model, only consumer species evolve, that is, m is an evolving trait. The resource does not evolve throughout this work.

3. Interference competition

The section is devoted to a biological outline of how to model interference competition in a size-structured population model at the individual-level. Detailed mathematical formulation of interference is presented in Appendix B.

Interference is assumed to occur when two similar individuals encounter one another. Here "similar" means that the two individuals have similar body size and similar trait value. Moreover, encounters between a focal individual and another individual can happen either when the focal individual encounters the other individual or vice versa. As the volumetric search rate is

increasing function of size, it is expected that the larger individual encounters the smaller individuals. According to the effects of interference on individual performance and population dynamics, we consider the following four types of interference competition.

1. Foraging interference, i.e. reduction in foraging rate. Interference leads to reduction in the time available to search for prey. Mathematically, the volumetric search rate is reduced by a factor τ_c, or equivalently, that $v(w) = \gamma w^q$ is replaced by $(1-\tau_c(w))\gamma_c \gamma w^q$. γ_c can be interpreted as the ratio of volumetric search rate between interference encounter and foraging encounter, and is a free parameter.
2. Metabolism interference, i.e. increase in metabolic costs or alternatively decrease in energy for growth and reproduction. Activity depletes energy and theoretical considerations of the cost of swimming activity found a scaling roughly proportional to individual body size (Ware, 1975). The cost of interference activity is $k_c \tau_c(w) w$, where k_c indicates the interference intensity, a free parameter. This cost should be added to the metabolic costs. As a consequence, individual somatic growth and reproduction are impaired to some extent.
3. Survival interference, i.e. death of individuals due to interference. The probability of dying from an encounter is assumed to be p_c, yielding an extra mortality $\mu_c = p_c / \Delta t_c(w)$ that should be added to individual mortality rate.
4. Recruitment interference, i.e. egg loss due to interference. We assume that individuals of any body size are able to prey upon eggs and that encounter with eggs is proportional to the individual encounter search volume. The recruitment is then quantified as $Re^{-\alpha_c f_e(w_0)}$, where R is the reproduced offspring (the right-hand side of equation (2)); α_c is a free parameter indicating the strength of interference.

Here, $\Delta t_c(w)$ means the fraction of time spent in interference encounter and τ_c the expected time between encounters. $f_e(w_0)$ indicates the encounter frequency between consumer individuals and eggs. The derivations of these formulas are left to Appendix B.

The interference parameters γ_c, k_c, p_c and α_c are nonnegative scalars whose ranges are hard to estimate due to the difficulty in disentangling interference competition and exploitative competition (Nakayama and Fuiman, 2010). Nonetheless, to facilitate the comparison of the effects of interference on population dynamics, each interference strength is scaled with a critical strength

value which is the strength of interference that makes the population biomass of a reference species fall below a certain level. Although the specific results depend on the choices of scaling method as well as the reference species, there is no qualitative influence since we are interested in whether small interference cost can incur great effects on the evolutionary dynamics. The reference species is chosen to be the species whose trait m_0^* is at an evolutionary equilibrium in the absence of interference. The threshold value that population biomass is reduced to is set to be one percent of the interference-free biomass. The results prove that our scaling effectively captures the fundamental role of interference in evolutionary speciation.

4. Results

Influence of the four types of interference competition on both population and communities are explored, respectively, in four subsections. In Subsection 4.1, we show the maturation size at evolutionary equilibrium in both a monomorphic and a dimorphic population environment, when interference is absent. The evolutionary equilibrium of maturation size m_0^* in a monomorphic population environment is selected as our reference species that is used to scale interference intensity. In Subsection 4.2, effects of interference on demographic properties of the reference species m_0^* are investigated. Subsection 4.3 demonstrates the adaption of evolutionary equilibrium maturation size m^* to interference strength ($m^* = m_0^*$ in the absence of interference). The last subsection considers the impacts of interference on species richness and trophic structure of the evolved communities that are obtained by solving the associated canonical equations (algorithm is referred to Appendix C).

4.1. Evolutionary equilibrium of maturation size without interference

As demonstrated in the fitness landscape of mutant invading the monomorphic resident population (Fig. 1), the point m_0^* is a local evolutionary attractor in the trait space. Species with maturation size smaller (larger) than m_0^* will evolve upward (downward) along the main diagonal to this attractor. During this course, mutants oust and take over the residents successively. Upon reaching m_0^* directional selection ceases and an evolutionary equilibrium is reached. This particular trait is the so-called evolutionary singular strategy in the context of adaptive dynamic theory (Geritz et al., 1998). At the singular strategy, disruptive selection takes over because this strategy is a local minimum on the fitness curve along the dashed line. Biologically it

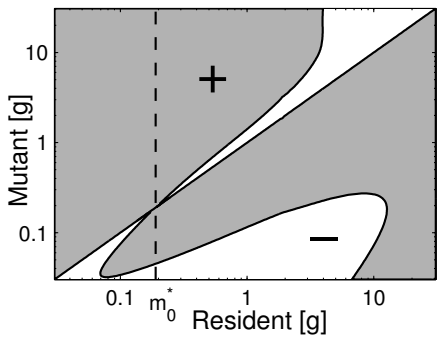

Fig. 1: Pairwise invasibility plot (PIP). Positive ("+") invasion fitness means mutant can invade the monomorphic resident population while negative ("−") means not. The point (dashed line) at which the main diagonal intersects with the boarders between positive and negative mutant fitness gives rise to the so-called evolutionarily singular strategy (Geritz et al., 1998). Invasion fitness is measured as the exponential growth rate of population biomass of mutant when rare (Metz et al., 1992). Parameter values are default in Table A.2.

means that mutants cannot outcompete but instead coexist with the resident, forming a protected dimorphism. The maturation size m_0^* is therefore evolutionarily unstable, and the monomorphic resident population undergoes an evolutionary branching.

After branching, the resident monomorphic population splits into two populations with distinct maturation sizes. As the coevolution of the dimorphic populations proceeds forward, the two traits diverge from each other following the direction indicated by the arrows in the two dimensional trait evolution plot (TEP) (Fig. 2). The following analysis is restricted to the bottom right half of the TEP since it is symmetric to the main diagonal. Once the dimorphism leaves the neighborhood of the initial branching point m_0^*, the evolutionary direction may change in the coexistence areas that are separated by the isoclines on which selection in one of the resident species is no longer directional. The two isoclines disappear when arriving at the boundary of the dark grey area before they meet together to form a dimorphic evolutionary equilibrium.

The deterministic evolving trajectory from the monomorphic to dimorphic equilibria is specified by the dashed line in Fig. 2. After branching,

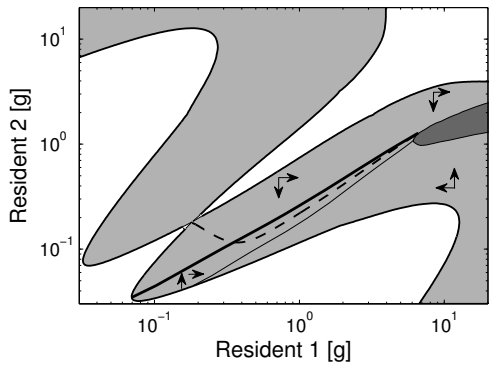

Fig. 2: Trait evolution plot (TEP). Light grey areas indicates the coexistence regions for resident species 1 and 2, where protected dimorphism is formed while dark grey area means that species 1 and 2 can invade one another when rare but cannot coexist. Thin (thick) solid line denotes the isocline where selection gradient ceases in resident species 1 (2), which is evolutionarily unstable (stable). The two isoclines vanish when meeting the dark green area before they could interact. Horizontal (vertical) arrows indicate the direction of evolution in resident species 1 (2). The plot is constructed from the PIP by overlapping the "+" areas of the PIP itself and of its mirror image taken along the main diagonal. The dashed line is the deterministically evolving trajectory, starting from the evolutionary monomorphism (m_0^*). The upper left half of the TEP is symmetric to the other part and thus not presented.

the emerging population with the smaller trait value evolves downwards and the other population evolves to the right, widening the gap between their trait values. Once the small trait crosses the thick solid isocline, the two populations stay within the region in between the isoclines until they reach the boundary of the unprotected area. Once coming to the boundary, one of them will go to extinction, but which species dies depends on whose trait first overshoots the boundary. Then, the system falls back to a lower level of polymorphism again.

4.2. Demographic properties of population m_0^* with interference

The demographic impacts of interference on population measures of species m_0^* are demonstrated in Fig. 3. Apparently, not all population quantities are

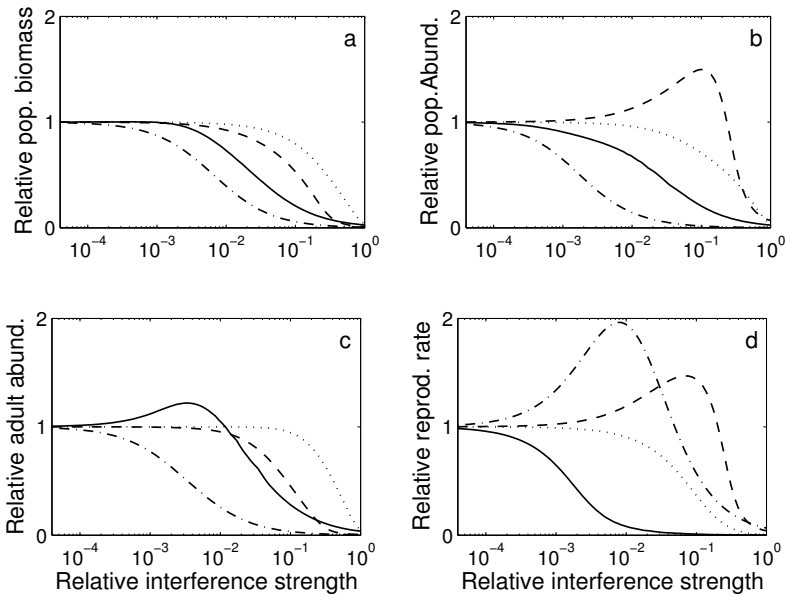

Fig. 3: The influences of interference competition as a function of the scaled interference strength on the demographic properties of species m_0^*: a) population biomass, b) population abundance, c) total adult abundance, and d) population reproduction rate. All demographic quantities are scaled in relation to the corresponding interference-free quantities. In case of oscillation, mean population quantities over long time were adopted. The curves in all panels represent foraging interference (solid), metabolism interference (dotted), survival interference (dashed), and recruitment interference (dash-dotted), respectively. Parameter values are default as in Table A.2.

negatively correlated with interference intensity and how they work depends on the underlying interference mechanism. The foraging interference increases adult abundance for a certain range of interference strength (Fig. 3c) while other quantities decline. The metabolism interference negatively affects population demographic properties. The survival interference, leading individuals to die, results in a considerable increase in population abundance as interference intensifies from a negligible value to a certain large value (Fig. 3b), although the population biomass declines within this range. Moreover, the increase results from the growth in juveniles since the adult abundance always drops (Fig. 3c). In stark contrast to the decrease in adult abundance is the rise in the population reproduction rate (Fig. 3d). The recruitment interference raises the population reproduction rate when interference intensity is small (Fig. 3d) while decreases other population quantities.

The net outcome between the costs due to interference and gains from resource accounts for above observations. No matter which mechanism is operating among organisms, there are always trade-offs between exploitative and interference competition. Interference incurs costs to all engaged individuals and therefore releases predation pressure on the resource. The released resource in turn makes more food available for consumer individuals. If an appropriate level of intensity is exerted, the net outcome could be positive. However, the net outcome varies with individuals and is not directly translated into population demographic properties but rather through creating a feedback loop via growth and fecundity. The feedback loop reshapes individual size distribution which determines population demographic quantities.

As an example, consider the survival interference. Interference raises individual mortality rate, lowers the population abundance, and thereby reduces the mortality rate on the resource. Consequently, surviving juveniles grow fast, compensating the loss of adult abundance. Population reproduction rate is the product of the adult size distribution and the associated size-dependent birth rate. When interference strength is week, the combined effect promotes the population reproduction rate. However, this advantage of resource availability is lost when survival interference intensity becomes strong.

4.3. Evolutionary equilibrium of maturation size with interference

The adaptive dynamics of the evolutionary equilibrium maturation size m^* in a monomorphic population environment with respect to interference intensity is shown in Fig. 4a. The four interference mechanisms affect the

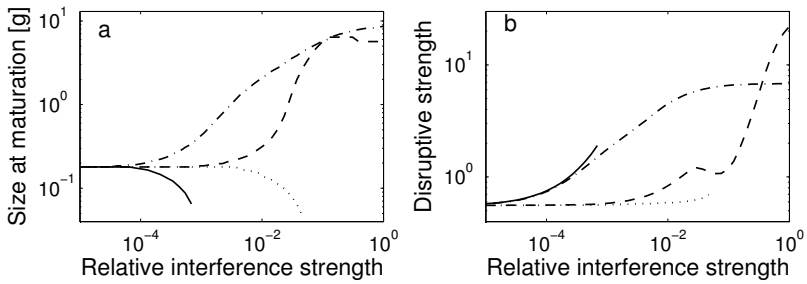

Fig. 4: Maturation size m^* at the evolutionary equilibrium (a) and the disruptive strength of the fitness function of the mutant invading the resident monomorphic population with trait m^* as a function of the relative interference strength (b). Disruptive strength was calculated by evaluating the second order derivative of the fitness function with respective to mutant trait at the resident trait m^*. Line styles and parameter values are the same as in Fig. 3.

evolution of the singular strategy in two distinguished manners. Precisely, foraging and metabolism interference drive the singular strategy down to the size at birth as interference intensity increases. On the contrary, the survival and recruitment interference drive up the singular strategy, postponing maturation to a larger size.

The disruptive strength at m^* is greater than the interference-free disruptive strength (Fig. 4b), implying that the four types of interference all promote evolutionary speciation, whereas the degree of promotion varies with the underlying mechanisms. Clearly, survival and recruitment interference are most likely to enable speciation while metabolism interference is the least. In combination with the monomorphic singular strategy m^* (Fig. 4a) yield two features: as interference strengthens, decreased size at maturation with remarkably increased disruptive strength for foraging interference but slightly for metabolism interference on the one hand, and increased size at maturation with enhanced disruptive strength for both survival and recruitment interference on the other.

The consequences of intensifying interference for the initial evolutionary equilibrium maturation size m^* result from the balance between interference induced cost and gain from released resource. Foraging interference reduces volumetric search rate, thereby lowing down the ability to consume the re-

source directly but increase resource availability as a compensation. However, the net effect is negative and maturation is delayed, suggesting cumulated mortality and low fertility rate. Evolutionarily, species with smaller maturation size is favored by natural selection. However, as a trade-off, total fecundity (number of eggs per female) decreases. As species evolves to size at birth, individuals would reproduce immediately after being born. This explanation also applies to the metabolism interference.

Quite the contrary, survival and recruitment interference accelerate individual growth rates due to the increase in resource availability that results from the decreased abundance of consumer individuals or alternatively alleviated exploitative competition. Maturation is thereby advanced, contributing to greater amount of offspring. To maximize this advantage, species evolves to larger species since large species have the potential of producing more offspring. Due to the size-related diet constraint, large individuals that have body size around β times greater than m_{cut} survive mainly on cannibalizing small juvenile individuals. However, larger maturation size means longer juvenile stage and larger metabolic costs for adult individuals. Once cannibals fail to obtain sufficient food to maintain metabolic costs, maturation size declines adaptively.

4.4. Community structure with interference

An example of evolutionary community assembly with survival interference is presented in Fig. 5. Through continuous branching, a community was eventually developed with 17 species settling on an evolutionary equilibrium (Fig. 5a). Among the emergent species, the largest one can be 1 kg, far greater than its ancestor. Species size spectra are shown in Fig. 5b, and their summation gives rise to the community size spectrum (Andersen and Beyer, 2006). As seen clearly, body size of large species covers a broad range, resulting in the shift of ontogenetic niche position due to the diet constraint on size. Characterizing species trophic level via the averaged trophic positions of adults makes it possible to graph the community trophic pattern (Fig. 5c), where up to four trophic levels were formed given that resource species sat on the trophic level of 1.

We concentrate on two measures with respect to the evolved communities: species richness and the maximum trophic level. Species trophic level is represented by the trophic position of adults since individuals within species may experience several trophic positions due to the ontogenetic trophic niche shift in their whole lives. The evolutionary responses of species richness and

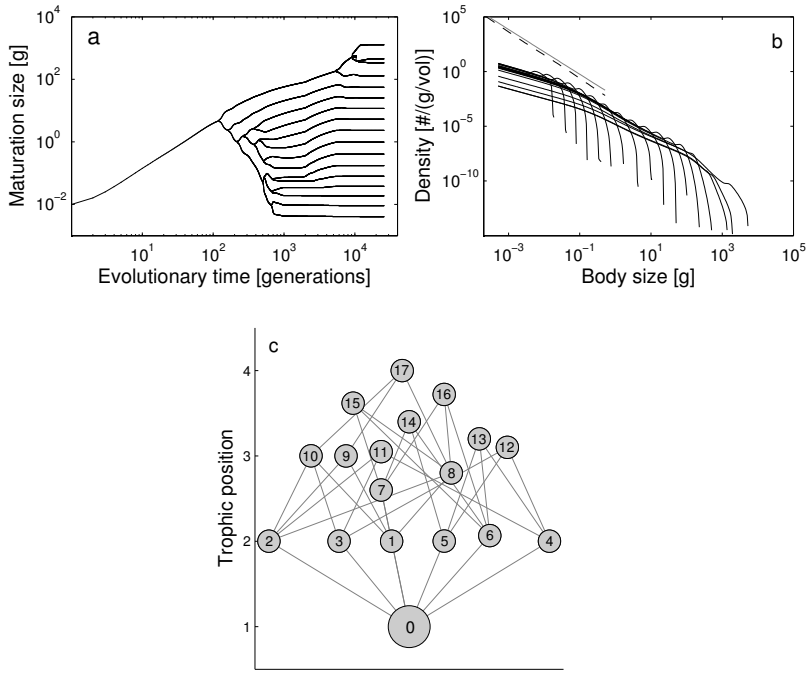

Fig. 5: An example of evolutionary community assembly for survival interference with relative intensity 0.2. a) The evolving trajectory of maturation size; b) Species size spectra (solid), together with the initial (gray) and final (dashed) resource size spectra at the evolutionary end-state, which is a fixed point in the trait space; c) Trophic levels of species (nodes) in the evolved community. Trophic level is defined to be the averaged path from a focal species down to resource (node 0), weighted by the proportion of energy along each path over the total energy that goes into the adult individuals of the focal species (Levine, 1980). A link from a prey to a predator is included if the prey makes a contribution of more than 15% to the total diet in a sampled predator stomach. Parameter values are the same as in Fig. 4.

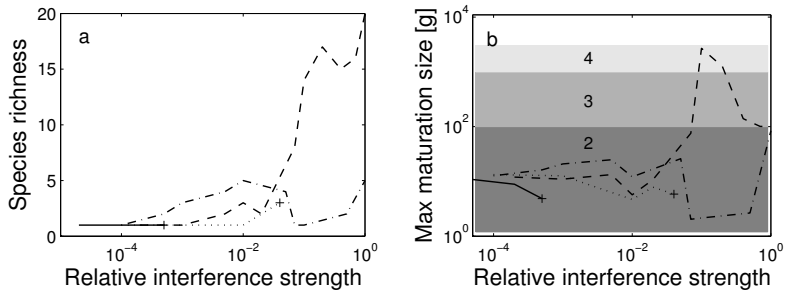

Fig. 6: Species richness (a) and the maximum maturation size (b) of the evolved communities as a function of the relative interference strength. Numbers in the distinct color bins denote the trophic levels that have been rounded off. The symbols "+" in the two panels indicate the endpoint for the foraging and maintenance interference competition. Line styles and parameter values are the same as in Fig. 4.

trophic structure of evolved communities vary with interference mechanism (Fig. 6). Remarkably, survival interference are more prone to yield large communities with high trophic levels, followed by recruitment interference. By contrast, foraging and metabolism interference can, however, only produce small communities consisting of a couple of small species and thus having simple trophic pattern. Moreover, comparing the species richness and trophic levels, it is interesting to see that the richest community does not have the highest trophic level. The reason is that the richest community consists of many small species.

5. Discussion

Adaptive dynamics of size-structured populations models has received much less attention than unstructured population models. Several existing studies either do not account for the effects of environment on individual life-history performance (e.g. Taborsky et al., 2003; Gårdmark and Dieckmann, 2006), or focus only on the initial branching point (e.g. Claessen and Dieckmann, 2002). What happens after branching has never been explored to our best knowledge. The paper presented here not only modeled the ecological feedback of environment on individual ontogentic growth, but also explored how

the frequency- and density-dependent selection drive the development of food webs.

In case that interference competition is absent, a curious finding is the region in which the two resident species can invade one another but fail to coexist (dark grey area in Fig 2). It seems inconsistent with the assumption made in the framework of adaptive dynamics that once each polymorphic resident population is protected against extinction by a positive growth rate when rare, a polymorphism is always supposed to be protected (Geritz et al., 1998). The reason for making this assumption is that it entails a purely simple description of which population remains once the environment has settled in new demographic attractor after being successfully invaded by a new mutant. Indeed, in the neighborhood of the singular strategy m_0^*, protected dimorphism was formed locally. Switching from unstructured population models to fully nonlinear size-structured population models, situation can potentially undergo qualitative changes. Thus, it is worth more efforts to elaborate this finding.

Interference architecture

Interference competition is a ubiquitous scenario among species (Case and Gilpin, 1974). The presented mechanisms are just four of a variety of interference forms that are widely observed in nature. For instance, diverting time from foraging for resource (foraging interference) has been seen from the vigilance of wading birds (Vahl et al., 2005). The behavior is to avoid fighting which may expose the birds to be on the risk of injury or even death. As a consequence, time devoted to search for food is reduced and feeding rate decreases subsequently. A common feature of these mechanisms is the dependence of interference on population densities, while density-independent interference, e.g. morphological interference recognized by Case and Gilpin (1974), is, however, excluded in this work.

The assumption that interference competition occurs between individuals with similar body size and trait value is crucial in our model. There are two direct ecological interactions among individuals, that is, interference competition and predation. As both interactions are quantified with body size, when there is a large difference between individuals predation dominates, otherwise interference dominates. An exception is the recruitment interference in which size does not matter any longer, because eggs do not swim and any individuals are able to prey upon them. However, both ecological

interactions are dynamically density-dependent. A difference between interference and predation is that while the latter is completely size-based, the former is additionally supposed to take place between similar species. This assumption introduces an asymmetry between interference and predation to ensure that predation is the main forcing of driving population dynamics.

The four interference competition were investigated separately in order to clarify the role of each mechanism in evolutionary speciation, but in reality they can take place simultaneously. An empirical support is the two filter-feeding copepod species *Diaptomus tyrrelli* and *Epischura nevadensis* inhabiting the Lake Tahoe. In laboratory experiments, Folt and Goldman (1981) found that *Epischura* not only produces allelopathy (a kind of chemical warfare) to reduce the feeding rate of *Diaptomus* (down to 60%) but also predates against nauplii and small copepodids of *Diaptomus* . What is unclear is the correlation between distinct interference mechanisms. Yet it remains unknown which mechanism exerts a dominant effect. Answers generally depend on targeted interfering species, but it is widely thought that a generalist is superior in a number of mechanisms while specialist excellent in a single mechanism (Case and Gilpin, 1974).

Ecological impacts of interference competition

The four types of interference competition cause direct negative costs on engaged individuals, which leads to the decline in the overall population biomass (Fig. 3). However, the negative effects can be compensated by the feedback loop created by individual growth and fecundity, which accounts for the increased demographic quantities, although the compensation varies with underlying interference mechanism. Such indirect benefits cannot be realized in unstructured population models unless assumed in priori. Taking into account both detrimental and beneficial interference in unstructured population model, Amarasekare (2002) predicted that species engaged only in costly interference may not be able to coexist unless beneficial interference mechanisms are included. A promising extension is how the presented interference competition affects the coexistence of size-structured populations and the results can be a valuable supplementary to the finding that predation and exploitative competition have equivalent potential to maintain species diversity (Chesson and Kuang, 2008).

Interference on the evolution of maturation size

According to the effects on the evolution of size at maturation, the four types of interference competition can be functionally classified into two categories. In the first category are the foraging and metabolism interference which directly affect individual physiology negatively, either by reducing foraging rate or by increasing extra energy depletion. Even though individuals are compensated by the enhanced resource availability, the net outcome is, however, negative. In the second category are the survival and recruitment interference which affect individual physiological rates only indirectly but positively. Decreasing individual abundance not only mitigates the exploitive competitions among consumer individuals but also relieves the predation mortality on resource. The consequence is that surviving individuals are able to experience more food, leading to an increase in the rates of growth and fecundity considerably. Although they all promote the disruptive strength of the branching point, the evolution of maturation size behaves in the different directions between the physiological-related and physiological-unrelated interferences.

In our size-structured population model, speciation can be initiated by ecological interactions of both predation and interference, although interference can intensify the disruptive strength of speciation. This finding agrees with Doebeli and Dieckmann (2000) who demonstrated that evolutionary speciation can arise from various ecological interactions including predation, competition, and mutualism in unstructured population models. Our result confirms once more that evolutionary speciation is a robust phenomenon, also in structured population models. However, it should be kept in mind that the present results relay on the given parameters in Table A.2. Even though the essential role of interference in promoting evolutionary speciation is reserved, distinct parameter sets might give rise to different evolutionary patterns.

As an extension, it is worthwhile to explore systematically how the evolutionary speciation is adapted to the various resource availability and to the relaxation of the assumption that interference takes place between individuals with similar trait values. These studies not only advance the understanding of interference competition in structured population models, but may also serve as a valuable and necessary complementation to the robustness of the phenomenon of evolutionary speciation.

Interference on the biodiversity of evolved communities

In the presence of interference interaction, rich and complex communities are able to be developed, signifying the evolutionary role of interference. However, not all interference mechanisms are evolutionarily beneficial. Survival and recruitment interference in general promotes the appearance of large communities but not the other two mechanisms. In comparison with the disruptive strength at the initial evolutionary equilibrium of maturation size (i.e. Fig. 4), there is no clear positive correlation between the diversity of evolved communities and the initial diversification, in consistence with the findings in unstructured population model (Brännström et al., 2010). However, a novel finding is that the richest community does not have the highest trophic level (Fig. 6). This observation is because many small species are needed to provide food for large species when survival interference is strong sufficiently.

In the example of evolved community (Fig. 5), the evolutionary end-state is a fixed point in the trait space, but it is not necessarily always the case. We did observe occasionally evolutionary limit cycles (Red Queen dynamics), but they were due to the restrict separation between the ecological and evolutionary time scales (Khibnik and Kondrashov, 1997). However, Red Queen dynamics can be triggered by diverse mechanisms, for instance, the predator-prey interactions (Dieckmann et al., 1995), alternative population dynamic attractors (Kisdi et al., 2001). Since in size-structured population model with abundant resource, alternative steady state may appear frequently (Hartvig and Andersen, 2012), interference may force population dynamics to switch between distinct ecological steady states, thus, potentially favoring the Red Queen dynamics (Kisdi et al., 2001).

Furthermore, interference competition is able to drive the emergence of large food webs (Fig. 5), whereas no possibility exists to form rich communities evolutionarily when interference is absent. In addition, by performing the ecological community assembly to our size structured population model without interference competition, it was found that only simple communities consisting of a couple of small species can be developed (Hartvig et al., 2011). These observations infer an important role of interference in the emergence of food webs.

Summary

Four types of interference competition were explicitly modeled for the first time in a continuously size-structured population model at the individual-

level processes. Ecologically, negative costs on engaged individuals are incurred directly, but positive effects come about once interference induced loss is overcompensated by the indirect gains caused by the feedback loop via life histories. Evolutionarily, although all promoting evolutionary speciation by strengthening the disruptiveness at the evolutionary equilibrium of maturation size, they differ in the ability of producing large food webs.

Acknowledgements

Lai Zhang was financially supported by the Danish Otto Mønsteds foundation and by the Ecology and Evolution Program at the International Institute for Applied System Analysis (IIASA).

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Appendix A. Size-structured population model

The model in Hartvig et al. (2011) provides a novel approach to construct food-web communities with continuously size structured populations. Species i is trait-based and characterized by size at maturation m_i. Individuals within this population are represented by body size w varying from w_0 to $M_i = m_i/\eta$. Here w_0 is the size of offspring, which is assumed to be uniform to all species, and M_i is the maximum attainable body size of individuals within population i. The distribution of individual abundance as a function of body size is termed as species size spectrum, denoted by $N_i(w,t)$ or simply by N_i. Lumping the size spectra of all species existing in a community gives rise to the community size spectrum (Andersen and Beyer, 2006), lifting the size spectrum from the species level to the community level consequently. Model equations and parameters are, separately, summarized in Table A.1 and A.2, and detailed description goes as follows.

Predation is size selective and mathematically formulated by a selection function (M1), which is a lognormal function (Ursin, 1973) that peaks when the size ratio of predator to prey equals the preferred predator-prey mass ratio β. The size range of prey individuals that a predator individual experiences is governed by the width of selection function σ. Thus, interactions between individuals with size ratio far from β are negligible.

Encountered food for w-sized individuals comes from predation upon resource and consumer individuals (M2), the amount of which is proportional to the size-dependent volumetric search rate (M3). Satiation is described by the feeding level (M3), which multiplied with the maximum food intake (M4) gives rise to the ingested food. With an assimilation efficiency α, ingested food is converted to energy (M6) that is utilized for life-history processes. Energy is in priority used for paying maintenance costs $k_s w^p$ and then, if there is any, used for individual somatic growth and reproduction. The distribution of the remaining energy between these two processes is governed by an allocation function (M7). The growth equation (M8) indicates that the surplus energy after paying metabolic cost is entirely used for juvenile growth but drops due to the onset of reproduction (M9). Individuals growth cease when they approach the maximum body size where all energy is routed to reproduction.

Besides the predation mortality (M10), individuals also suffer from trait-dependent background mortality, i.e. $\mu_0 m_i^{n-1}$, and starvation (M10) when assimilated energy is insufficient to cover metabolic costs. The total mortality

of w-sized individuals is thus $\mu_i(w) = \mu_p + \mu_0 m_i^{n-1} + \mu_s(w)$. Moreover, in case of starvation, growth and reproduction stop instantaneously. The addition of background mortality to system is to avoid unlimited growth in abundance of the largest individuals since they do not experience any predation.

Population dynamics is described using the McKendrick-von Foerster equation (1). The total reproduced offspring is recruited to species size spectrum to form the lower boundary condition of equation (2).

Resource is not trait-based. Its dynamics follows the chemostat growth (3). It is distributed continuously along the size direction and truncated at the size m_{cut}. The lower limit of resource size does affect results as long as it is far smaller than w_0. Both carrying capacity (M12) and regeneration rate (M13) are size-dependent. Mortality on resource stems only from predation by consumer individuals (M10).

For convenience, we introduce a reference weight $w_r = 1$ g to scale individual body size and the trait by setting $\tilde{w} = w/w_r$ and $\tilde{m} = m/w_r$, respectively. Such scaling brings with some scaling constants in the equations listed in Table A.1. For instance, the volumetric search rate $v(w) = \gamma w^q$ is transformed to $v(\tilde{w}) = \gamma w_r^q \tilde{w}^q$. The emergent constant w_r^q can be eliminated by defining $\tilde{\gamma} = \gamma w_r^q$. Other relevant equations and parameters are scaled in a similar way. To suppress excessive notations, the tildes are dropped in this paper. The parameters presented in Table A.2 have been scaled.

Appendix B. Modeling of interference competition

Interference competition is supposed to take place between individuals having similar body size and similar maturation size, mathematically formulated by a size interference kernel (B.1) and a trait interference kernel (B.2)

$$I_w(w/w') = \exp\left(-\frac{\log^2(w/w')}{2\sigma_w^2}\right), \tag{B.1}$$

$$I_m(m/m') = \exp\left(-\frac{\log^2(m/m')}{2\sigma_m^2}\right). \tag{B.2}$$

The consequences of the encounter can be a reduction of time spent searching for prey (foraging interference), an extra loss of energy for activity during encounter (maintenance interference), a risk of dying as a result of the encounter (survival interference), or extra mortality on eggs (recruitment interference). To estimate these effects it is necessary to evaluate the expected

Table A.1: Model equations

Num	Equation	Interpretation
M1	$\varphi(w/w') = \exp(-\log^2(w'\beta/w)/(2\sigma^2))$	Selection function
M2	$E(w) = v(w)(\int_0^{m_{cut}} w'R(w')\varphi(w/w')dw'$ $+\sum_j \int_{w_0}^{m_j/\eta} w'N_j(w')\varphi(w/w')dw')$	Encountered food from resource and consumers
M3	$v(w) = \gamma w^q$	Encounter search rate
M4	$F(w) = E(w)/(E(w) + I_{max}(w))$	Feeding level
M5	$I_{max}(w) = hw^n$	Maximum food intake
M6	$S(w) = \alpha I_{max}(w)F(w)$	Assimilated energy
M7	$\psi(w,m) = (1 + (w/m)^{-10})^{-1}(\eta w/m)^{1-n}$	Allocation function
M8	$g(w,m) = \max\{0, (1-\psi(w,m))(S(w) - k_s w^p)\}$	Individual growth rate
M9	$b(w,m) = \max\{0, \psi(w,m)(S(w) - k_s w^p)\}$	Individual birth rate
M10	$\mu_p(w) =$ $\sum \int_{w_0}^{M_j} v(w')(1-F(w'))N_j(w')\varphi(w'/w)dw'$	Predation mortality
M11	$\mu_s(w) = \max\{(S(w) - k_s w^p)/\xi w, 0\}$	Starvation mortality
M12	$\kappa(w) = \kappa_0 w^{-\lambda}$	Resource carrying capacity
M13	$r(w) = r_0 w^{n-1}$	Resource generation rate

time between encounters $\Delta t_c = l + 1/f(w)$ and the fraction of time spent in interference encounter $\tau_c = l/\Delta t_c$, where l is the length of an encounter and $f(w)$ is the frequency of encounters. It is assumed from metabolic theory (Gillooly et al., 2002) that each encounter takes time $l = t_c w^{0.25}$. The key issue of the interference competition is to model the frequency of encounters, i.e. $f(w)$. Encounters between a focal individual and another individual can happen either when the focal individual encounters the other individual or vice versa. As the search volumes are increasing functions of size, it is expected that the larger individual encounters the smaller ones. From these considerations the frequency of encounter by an individual of species i can be estimated as

$$\begin{aligned} f_i(w) &= \sum_j I_m(m_i/m_j)\left(\int_{w_0}^{w} v(w)I_w(w/w')N_j(w',t)dw'\right. \\ &\quad \left. + \int_{w}^{M_j} v(w')I_w(w/w')N_j(w',t)dw'\right). \end{aligned} \tag{B.3}$$

Here, the first (second) integral calculates the frequency at which the focal individual encounters individuals with size smaller (larger) than itself.

Table A.2: Model parameters and default values

Parameter	Value	Unit	Interpretation
Consumer			
β	100	$--$	Preferred predator-prey mass ratio
σ	1	$--$	Width of selection function
α	0.6	$--$	Assimilation efficiency
ε	0.1	$--$	Reproduction efficiency
h	85	g/year	Scaled prefactor of maximum food intake
k_s	10	g/year	Scaled prefactor of standard metabolism
n	0.75	$--$	Exponent of maximum food intake
p	0.75	$--$	Exponent of metabolic costs
q	0.8	$--$	Exponent of volumetric search rate
η	0.25	$--$	Ratio of maturation size to maximum size
μ_0	0.84	g/year	Scaled background mortality
ξ	0.1	$--$	Fraction of energy reserves
w_0	0.0005	$--$	Scaled egg size
f_0	0.6	$--$	Initial feeding level
γ	$\frac{f_0 h \beta^{2-\lambda} w_r}{\sqrt{2\pi}(1-f_0)\kappa_0 \sigma}$	g/year	Scaled factor of volumetric search rate
w_r	1	g	Reference weight for scaling[§]
Resource			
κ_0	0.005	$\mathrm{g}^{-1}/\mathrm{m}^3$	Scaled magnitude of resource size spectrum
r_0	4	1/year	Scaled generation rate
m_{cut}	0.5	$--$	Upper limit of resource spectrum
λ	$2+q-n$	$--$	Slope of resource spectrum
Interference competition			
t_c	1	$--$	Scaled factor of encounter time[‡]
σ_m	0.5	$--$	Width of interference kernel in trait direction[†]
σ_w	0.5	$--$	Width of interference kernel in mass direction[†]
σ_μ	0.05	$--$	Standard deviation of mutation step[¶]
μ_m	0.001	$--$	Mutation probability per birth event[¶]

[§]Arbitrary; [‡]Set to be 1 for simplicity. [†]Small values in relative to σ to ensure that interference occurs among individuals with similar body size and similar trait value. [¶]Dieckmann and Doebeli (1999). The remaining are from Hartvig et al. (2011).

The time between encounters is $1/f(w)$. From these two quantities we can evaluate the time between encounters and the fraction of time spent during encounters as

$$\Delta t_c(w) = t_c w^{0.25} + 1/f(w), \tag{B.4}$$
$$\tau_c(w) = t_c w^{0.25}/\Delta t_c(w). \tag{B.5}$$

Among the four types of interference competition, the mechanism of recruitment interference differs from others. We assume that eggs of species i can be interfered against by individuals of any body size but with similar trait values. Mathematically, the size kernel (B.1) disappears in the calculation of frequency, that is,

$$f_{e,i}(w_0) = \sum_j I_m(m_i/m_j) \int_{w_0}^{M_j} v(w) N_j(w,t) dw. \tag{B.6}$$

Values of parameters t_c, σ_w and σ_m are given in Table A.2.

Appendix C. Evolutionary community assembly

Communities are obtained using evolutionary community assembly. The evolutionary trajectory of a species is deterministically determined by a canonical equation (Dieckmann and Law, 1996)

$$\frac{dx}{dt} = \frac{1}{2}\mu_m \sigma_\mu^2 R(x) \partial_y S_x(y)|_{y=x}, \tag{C.1}$$

where x and y are the logarithmical values of the traits of resident and mutant. μ_m is a small mutational step with a standard deviation σ_μ that determines the similarity of mutant and resident species. $R(x)$ is the reproduction rate of resident species while $S_x(y)$ is the fitness function of mutant y invading resident x, with invasion fitness being measured by the exponential population growth rate (Metz et al., 1992). $S_x(y)|_{y=x}$ gives the selection gradient at x. Positive gradient means that species x will evolve to larger species and vice versa. An important case is that the gradient vanishes. A trait with vanishing selection gradient is called evolutionary singular strategy that graphically is either a minimum or maximum on the fitness curve defined by $S_x(y)$. Being a minimum (positive curvature of the fitness curve at the singular strategy) implies that the singular strategy is evolutionarily unstable and speciation takes place. In multi-species environment, if all

species are maxima then no speciation occurs suggesting that the community has reached a evolutionary steady state (ESS).

Assembly starts from the environment where the resource and ancestor are at demographic steady state and the trait of the ancestor is slightly smaller than the evolutionary equilibrium in a monomorphic environment. The algorithm is given as follows.

1. Suppose there are multiple species in the current environment with traits being denoted by $x = (x_1, \cdots, x_n)$. Each species is governed by a canonical equation (C.1) and a McKendrick-von Foester (MvF) equation (1). Do numerical integration until the environment reaches demographic steady state.
2. Evaluate the selection gradient of each species x_i, i.e. $\partial_y S_x(y)|_{y=x_i}$. There are three cases: (i) Non-vanishing gradient. A mutant with a trait of $x_{n+1} = x_i + D(x_i)$ is added to the environment. Meanwhile, a new canonical equation is added to trace its evolving trajectory and a new McF equation to describe its demographic dynamics. $D(x_i)$ is the evaluation of the right-hand side of equation C.1. (ii) Vanishing gradient with negative curvature. There is nothing to do with this resident species. (iii) Vanishing gradient with positive curvature. It means that this resident species has reached a branching point. In this case, two mutants emerge symmetrically, i.e. x_{n+1} and x_{n+2} are $x_i \pm \delta$, where δ is chosen at random from a Gaussian distribution with mean value 0 and standard deviation σ_μ^2. In addition, two canonical equations and two MvF equations are added.
3. If all species have vanishing gradients with negative curvatures, then assembly ceases. Otherwise, go back to step 1.

Actually, there is one more case in step 2, that is, both the gradient and curvature are zero. This case is extremely rare and thus ignored. We assume a strict separation between the ecological and evolutionary time scales (Doebeli and Dieckmann, 2000) with ecological dynamics proceeding faster than the evolutionary dynamics, meaning that the resident community dynamic has settled on its ecological attractor before mutant appears. During assembly, population biomass of mutant is initially set to be 10^{-20} g/vol that is also viewed as an extinction threshold value. Values of parameters σ_μ and μ_m are given in Table A.2.